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UNIVERSITY OF ALBERTA

The Hominid Masticatory System: A Biomechanical Analysis

BY

Penelope E. Grey

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE
OF................Doctor of Philosophy.................

IN
Oral Biology

Faculty of Dentistry

EDMONTON, ALBERTA
(SPRING, 1990)

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ENTITLED.........The Hominid Masticatory System: A Biomechanical Analysis.........................

SUBMITTED BY.....Penelope E. Grey...............

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF....Doctor of Philosophy...........

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DEDICATION

To my family, for their patience and support.

ABSTRACT

Because the most important function of the masticatory system is to break up food, apparently large differences between the masticatory systems of hominids have been attributed to differences in diet. A mechanical approach was applied to a selection of extinct and extant hominids in order to detect whether or not there may have been differences in the way they broke up food. A mathematical computer assisted model of the jaw was applied which predicted the combination of muscles used to produce an efficient bite force. Efficiency was measured by the ratio of bite force to total muscle force. Torques at the symphysis were subsequently calculated for selected bite forces. Finally, a three dimensional model of jaw closure was applied that allowed the calculation of maximum crush:shear ratios for the first molar. The most important conclusions included the following. (1) The masticatory systems of the hominids are broadly similar, indicating that they probably had broadly similar diets. (2) Hominids from different taxa could not be distinguished by the mechanics of their masticatory systems. (3) The evolution of hominid jaws was not solely concerned with improving the moment arms of masticatory muscles. (4) Australopithecus and Homo could not be distinguished by their patterns of symphyseal torque. (5) The range in the diets of early Homo and Australopithecus may have differed, considering the differences in their maximum crush:shear ratios.

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CHAPTER 1 INTRODUCTION

The masticatory systems of almost all mammals contain a heterodont dentition set in bony jaws, muscles which move the lower jaw with respect to the upper, and articulations between the lower jaw and the cranium about which this movement takes place - the temporomandibular joints (TMJs). Despite this common plan the morphology of each of these parts differs between and within mammalian taxa and this has been attributed to the functional demands of different diets (Becht, '53; Turnbull, '70; Noble, '80).

The most important function of the mammalian masticatory system is to break up food, a mechanical process best understood by applying the laws of mechanics. No amount of measurement or description of its parts will reveal its function, just as the design and operation of a wrench cannot be explained by measuring its size or describing its shape. It is an engineering problem whose solutions depend upon mathematical analyses.

A. Goal of the Present Study

The goal of the present study was to determine whether or not the morphological differences between various extinct and extant hominids could be related to mechanical differences in the way they broke up food. Two mathematical models were applied. The first was a computer assisted model based on linear programming. It was used to determine the most efficient combination of masticatory muscles to produce a bite force, that is, the one which minimized the total muscle force. The results of this investigation were then used to calculate torque at the mandibular symphysis for selected bite forces. The second model held that a tooth moves on the surface of a sphere centered at the condyle. It was used to determine the maximum ratio of vertical to non-vertical components of the path of the first molar during jaw closing (the maximum crush:shear ratio). The assumption was that the ratio was related to the properties of the diet.

The models were developed at the University of Alberta by J.W. Osborn of the Department of Oral Biology and F.A. Baragar of the Department of Mathematics.

B. Mechanics of the Human Masticatory System

From a mechanical point of view the mandible is a rigid body withstanding effort forces and resistance forces and rotating around one or more of its points of contact with the cranium. The effort forces are produced by the muscles of mastication and the resistance forces are applied at the dentition and the TMJs.

Because the mass of the mandible and its acceleration during closing are small, the effort forces required to move the jaw are insignificant compared to those used to break up food. In mechanical terms, therefore, the masticatory system is in static equilibrium. For static equilibrium the sum of the forces on the mandible must be zero and the sum of the torques (moments) produced by those forces about a fixed point in space must also be zero.

Because the resultant effort force usually lies between the load (at the dentition) and the fulcrum (at the TMJs), the mandible is considered a Class III lever (Fig. 1). The mechanical advantage of a Class III lever is always less than one because the length of the resistance arm exceeds the length of the effort arm.

To satisfy the conditions of static equilibrium there must be forces at the TMJs. The joints are offloaded only if the muscle resultant is parallel to the bite reaction force and passes through the bite point.

1. The Sagittal Projection

For biting on the incisors and for symmetric bilateral biting (clenching) on the postcanine teeth, the system is analysed in the sagittal projection (Fig. 2). The resultants of the muscle, bite reaction and joint reaction forces lie in the sagittal plane. Their magnitudes are calculated using the equations of static equilibrium. In the sagittal projection the mechanical advantage of the system is improved by 1) increasing the distance between the line of action of the resultant muscle force and the joint, thereby lengthening the effort arm, 2) decreasing the distance between the bite point and the joint, thereby shortening the resistance arm, or 3) both. Maximum bite force efficiency - the largest ratio of bite force to muscle force - exists in a Class III lever system if the joints are offloaded, by superimposing the muscle resultant and the bite reaction force.

2. The Frontal Projection

Man habitually breaks up food on one side of the mouth at a time, so in reality the bite point or the resultant bite reaction force is not located in the sagittal plane. Further, electromyographic studies have shown that during unilateral biting the muscles of the working side (w.s.) are more active than those of the balancing side (b.s.) (Moller, '66). The muscle resultant thus lies on the w.s. of the sagittal plane, and a greater share of the joint reaction force may fall on the b.s. condyle (Hylander, '85).

The position of the muscle resultant depends on the w.s. and b.s. muscles used and their activity. The magnitudes of the forces are calculated using the equations of static equilibrium. In the frontal projection (Fig. 3) the mechanical advantage of the system is improved by 1) increasing the distance between the condyles, thereby lengthening the effort arm, 2) decreasing the width of the dental arch, thereby shortening the resistance arm, or 3) both. Forces at the joint are again eliminated if the muscle resultant and the bite reaction force are superimposed. However, the bite force is reduced because the total muscle force is reduced - the activity of the w.s. muscles must exceed that of the b.s. muscles.

3. The Occlusal Projection

In the occlusal (transverse) projection a triangle of support is formed by the bite point on the dentition and the two condyles (Fig. 4). For static equilibrium the points of application of muscle resultant, bite force and combined joint forces must lie in a straight line. For symmetric bilateral biting the resultants lie in the sagittal plane, the forces being equally distributed between left and right sides. For unilateral biting, the position of the muscle resultant and that of the joint reaction resultant depend on the w.s. and b.s. muscles used and their activity. For example, if the activity on the b.s. exceeds that on the w.s. then the b.s. condyle bears the larger force (see Fig. 4). The w.s. or b.s. condyle is offloaded if the activity of the muscles and the position of the bite point are carefully manipulated. Both condyles are offloaded if the muscle resultant and bite reaction force are superimposed, but the bite force is reduced.

C. The Literature - Human Jaw Mechanics

The goal of mechanical analyses of the masticatory system is to determine how the masticatory system works. Researchers using this approach investigate the relationship between muscle, bite and joint forces within the system. In the following pages some of the important contributions to that end are described. The reader is referred to the reviews of Barbenel ('69), Hylander ('75, '85) and Smith ('78) for earlier papers. These authors addressed a long standing issue in the study of jaw function - whether or not there are forces at the TMJs. To summarize, those workers that believed the joints are not loaded during function presented three main arguments.

(1) The tissues of the TMJ are not designed to withstand forces.

(2) The resultant of the muscle forces passes through the bite point, thereby eliminating forces at the joint.

(3) The Class III lever arrangement is inefficient. More force is expended by the masticatory muscles than resisted at the bite point because the mechanical advantage is always less than one.

The evidence presented to support these arguments was, however, discounted by the reviewers for the following reasons.

(1) The condyle is firmly seated against the articular eminence during biting, rather than against the roof of the mandibular fossa (as had been assumed). The bony and soft tissues of the region are well suited to withstand stress.

(2) In constructing their force diagrams many workers have a) ignored the effects of some muscles in favor of others, b) ignored the effects of certain components of the muscles, c) misrepresented the position of the muscle resultant, d) incorrectly defined a couple, e) arbitrarily chosen one bite point and excluded others, or f) arbitrarily chosen a bite force direction or considered only a vertical bite force.

(3) During evolution an organism with a design only a little better than its competitors has a better chance of surviving. Evolution therefore does not shoot for an optimal design. There are many so-called inefficient Class III lever arrangements in the body.

The reviewers concluded that, though one or both of the condyles can be offloaded under certain circumstances (see previous section), there are usually forces at the joints during jaw function.

A mathematical analysis of the masticatory system requires that all attributes of the forces in the system - their magnitudes, directions and points of application - be incorporated into it. Some of these must be estimated and others manipulated, so that one or more can be calculated, as indicated in the studies described below. The attributes of the joint forces can never be directly measured in humans, while those of the muscle and bite forces have been estimated using various techniques. All three forces can never be measured at once. Thus, researchers interested in how the masticatory system works have turned to jaw modeling.

All of the studies examined below have made a contribution to our understanding of jaw function. However, two important facts must be considered.

(1) The masticatory system is three dimensional and can only be realistically represented by a model that operates in three dimensions.

(2) None of the forces can, with acceptable accuracy, be directly measured in humans, so all of their attributes are in fact unknown. When the jaw is modeled, therefore, these attributes are, at best, estimated.

With these two facts in mind, the following was noted of the studies described below.

(1) The analyses were often limited to the sagittal projection and thus simulated bilateral biting (Barbenel, '69; Pruim *et al.*, '80, Throckmorton, '85; Throckmorton and Throckmorton, '85; Osborn and Baragar, '85). Humans, however, habitually bite unilaterally. Unilateral bites were simulated in some studies but were analyzed in two projections separately (Gysi, '21; Smith *et al.*, '86). In others they were simulated *and* analyzed in three dimensions and thus represented the masticatory system more realistically (Barbenel, '72; Hatcher *et al.*, '86; Faulkner *et al.*, '87; Koolstra *et al.*, '88; Hannam and Wood, '89).

(2) With regard to muscle forces:

a) The number represented varied from one (Hannam and Wood, '89) to 24 (Osborn and Baragar, '85), severely limiting the comparability of the studies.

b) In those studies where muscle magnitudes were not one of the unknowns, they were either arbitrarily chosen (Smith *et al*., '86), estimated from EMG activity (Barbenel, '69; Throckmorton, '85; Throckmorton and Throckmorton, '85;) or set at maximum according to cross sectional area (Gysi, '21; Koolstra *et al*., '88; Hannam and Wood, '89). Pruim *et al*. ('80), Hatcher *et al*. ('86) and Faulkner *et al*. ('87) used both EMG activity *and* cross sectional area. Smith *et al*. ('86) manipulated their magnitudes to find a combination that minimized the joint force. Koolstra *et al*. ('88) successively minimized the most active muscle to maximize the bite force. Osborn and Baragar ('85), on the other hand, set a maximum magnitude for each muscle, but solved for the combination used to produce a bite force.

c) In every study each muscle force was represented by a straight line drawn between its origin and insertion. The line represented its average line of action. Thus far this practice has been considered acceptable, with the knowledge that the *possible* lines of action of the masticatory muscles are minimally represented.

(3) With regard to bite forces:

a) The bite force was usually manipulated - a number of magnitudes, directions and bite points being considered. This is reasonable because the bite force depends on the properties of the diet and governs the muscles chosen to produce it.

b) In some of the studies only vertical bite forces were considered (Gysi, '21; Barbenel, '69; Pruim et al., '80; Osborn and Baragar, '85; Throckmorton, '85; Throckmorton and Throckmorton, '85; Hatcher et al., '86; Hannam and Wood, '89).

(4) With regard to joint forces:

a) In most of the studies one or more attributes of the joint force were calculated. For some, the direction was specified and the magnitude calculated (Gysi, '21; Pruim et al., '80; Osborn and Baragar, '85; Koolstra et al., '88). For others, both the direction and magnitude were calculated (Barbenel, '69, '72; Throckmorton, '85; Throckmorton and Throckmorton, '85; Hatcher et al., '86; Faulkner et al., '87; Hannam and Wood, '89). Smith et al. ('86) calculated the minimum joint force and Koolstra et al. ('88) calculated the joint force associated with the maximum bite force.

b) The direction of the joint force was presumed to be perpendicular to the condyle in some studies (Pruim et al., '80, Osborn and Baragar, '85, Koolstra et al., '88). This is valid because the condyle must be stabilized on the eminence. However, the articular surface of the condyle is irregular in shape. The direction in space of the perpendicular force can thus vary depending on the point of application of the force. That point was rarely defined (Pruim _et al_., '80; Throckmorton and Throckmorton, '85; Koolstra _et al_., '88).

All of the studies mentioned above are described below in more detail so that comparisons are facilitated. Most of them involved the calculation of magnitudes and directions of joint forces (Gysi, '21; Barbenel, '69, '72; Pruim _et al_., '80; Throckmorton, '85; Throckmorton and Throckmorton, '85; Smith _et al_.; Hatcher _et al_., '86; Faulkner _et al_., '87). Others focused on the magnitudes and directions of bite forces (Koolstra _et al_., '88; Hannam and Wood, '89). The emphasis of Osborn and Baragar ('85) was on the way in which the muscles were recruited to produce a bite force.

1. Joint Forces

One of the earliest analyses was done by Gysi ('21), who simulated bilateral and unilateral biting on reconstructions of the human jaw - first on paper, then on a mechanical model. For the mathematical analysis the magnitude of the muscle resultant was arbitrarily chosen and its point of application was estimated. Only the vertical components of all the forces were considered. The magnitudes of the bite and joint forces were calculated for several bite points.

For the mechanical model the maximum tensions of the four muscles were estimated from cross sections of dissected muscles and they were represented by springs, attached to a wooden model according to their estimated directions. The results showed the following.

(1) The bite force increased and the joint force decreased as the bite point shifted posteriorly.

(2) For symmetric bilateral biting the bite force and the joint force were equally distributed between the two sides.

(3) For unilateral biting, with the w.s. and b.s. muscles exerting equal forces, the forces of the b.s. muscles were distributed between the b.s. condyle and the symphysis. They were transmitted through the symphysis to the bite point on the w.s.. Regardless of the position of the bite point, the force on the b.s. condyle was about one-third of the total (bite?) force. The more posterior the bite point, the less force there was on the w.s. condyle. When biting on the second molar there was no force on the w.s. condyle and when biting on the third molar the w.s. condyle was distracted.

(4) The w.s. joint force was reduced and the bite force increased during unilateral biting when compared to bilateral biting.

Barbenel ('69) simulated symmetric bilateral biting on the incisors. The magnitudes of the three jaw closing muscle forces were estimated from their EMG activity in human subjects. Their directions and points of application were estimated from dissection. The direction of the bite force was assumed to be vertical. The magnitude of the bite force and the magnitude and direction of the joint force were calculated. The effect of adding lateral pterygoid to the equation was recorded.

(1) With increased activity of the lateral pterygoid the vertical component of the joint force decreased while the horizontal component increased.

(2) Without the lateral pterygoid, the direction of the joint force was downward and backward at an angle of nearly 30 degrees to the vertical.

In a subsequent paper Barbenel ('72) used linear programming to test two models of jaw function. One minimized the force at the TMJs and the other minimized the total muscle force. Muscle force magnitudes and magnitudes and directions of joint forces were calculated for symmetric bilateral biting at a number of bite points and for a number of bite force directions.

When the joint force was minimized the results showed the following.

(1) The joints were loaded when the angle of the joint reaction force to the vertical was greater than fifteen degrees.

(2) The magnitude of the joint force increased as the angle between the direction of the bite force and the

vertical to the occlusal plane increased.

(3) The magnitude of the joint force increased as the distance between the bite point and the condylar axis increased.

When the total muscle force was minimized the joint force was even larger.

(1) For small distances of the bite point from the condyle, increases in the bite angles from the vertical increased the joint force, while for large distances the load fell.

(2) The joint force was smallest when the bite point was closest to the condyle.

Barbenel ('72) rejected the first model, minimizing the joint load, because the joint was almost always loaded. The second model, minimizing the total muscle force, was rejected because it showed that only the masseter muscle acted during biting.

Pruim _et al_. ('80) presented a model which allowed calculation of muscle forces and joint forces during symmetric bilateral biting. EMG activity of the masseter, anterior and posterior parts of the temporalis and the jaw opening muscles, and vertical bite forces were measured on seven male subjects. A value 'Γ' was defined as the maximum force in a muscle (determined from the EMG data) divided by its cross sectional area (based on Schumacher's ('61) and Carlsoo's ('52) data). It was calculated by incorporating the EMG and bite force data in the moment equation. The forces in each pair of muscles were then calculated and the forces in the joints and the lateral pterygoid were subsequently calculated. The directions and points of application of the forces were derived from cephalograms of the subjects. The bite points PM1, M1 and M2 were investigated. The direction of the joint force was assumed to be perpendicular to the articular surface of the condyle. The results showed the following.

(1) 'Γ' was independent of the bite point, and its average value was 13.7kg/cm^2.

(2) Judging by their moments, the opening muscles (in the floor of the mouth) had an important role and the anterior and posterior temporalis behaved differently.

(3) The direction of the muscle resultant was tilted forward as the bite point shifted anteriorly.

(4) A nearly linear relationship existed between the force of the lateral pterygoid muscle and the bite force moment.

(5) The joint forces were larger when biting on the first premolar than on the second molar.

(6) The maximum bite force was exerted on M1. The bite force moments at PM1 approached those at M1, and those at M2 were low. The optimum bite point was located at or close to M1.

(7) Maximum forces never occurred in all of the muscles

simultaneously in the same bite recording.

(8) The relationship between the joint forces and the bite force moments was nearly linear.

Throckmorton ('85) and Throckmorton and Throckmorton ('85) used a two dimensional, two muscle model of the human jaw. The goal was to determine the importance of the magnitude and direction of the temporalis and masseter muscle forces in calculations of the magnitude and direction of the joint force. The initial values of the variables, about which increments of change were taken, were derived from a single subject. The ratio of the magnitudes of the muscle forces was estimated from their EMG activity. The directions of the muscle forces and the points of application of all the muscle forces were measured on a cephalogram of the subject. Vertical bilateral bites of 20kg were simulated. The magnitude and direction of the joint force was calculated. The change in each variable was plotted against the change it produced in the joint reaction force. The results showed the following.

(1) There was a linear relationship between bite and joint force magnitudes, the slope of the line varying with the relative lengths of the bite and muscle force moment arms. Bite force magnitude had no effect on the direction of the joint force.

(2) The direction of the joint force approached 90 degrees when bite and muscle force moment arms were

significantly different. It changed rapidly when they approached equal length.

(3) Changes in the ratio of temporalis to masseter force had little effect on the magnitude of the joint force, but a greater effect on its direction. When their forces were equal the direction was vertical. As masseter force became more dominant, it was more posteriorly directed, and as temporalis became more dominant it was more anteriorly directed.

(4) For incisor biting, muscle moment arms had a large effect on the magnitude of the joint force (and decreased it), especially if they were short. As muscle and bite force moment arms approached the same length the effect was decreased. Muscle moment arms had little effect on the direction of the joint force. For molar biting, the direction changed quickly as bite and muscle moment arms approached the same length.

(5) When the directions of the two muscles were changed by rotating them on the lever arm (a line parallel to the occlusal plane and passing through the condyle), the direction of the joint force shifted in the direction opposite to that of the change in the muscle force direction. The rate of change was greater for molar biting than for incisor biting. It was also greater when both muscles were changed in the same direction. It had little effect when they were changed in opposite directions, since

their resultant remained the same.

(6) The effect of rotating the muscles around points not on the lever arm had variable effects on the magnitude and direction of the joint force. In general the vertical position of the point of rotation had a smaller effect than its horizontal position because of the different effects these had on moment arm lengths.

To summarize, the magnitude and direction of the joint reaction force was most sensitive to the relative moment arms of the bite and muscle forces. They were also sensitive to the directions of the muscle forces.

Smith _et al_. ('86) investigated TMJ loading using a model which involved the minimization of joint forces. Any force acting on the condyle, independent of its direction, was a condylar force. The combination of muscle forces to minimize the condylar force for a given bite force was determined in the sagittal plane by arbitrarily assigning magnitudes and manipulating one muscle at a time. The equations of static equilibrium were first solved in the sagittal plane, and then in two additional perpendicular planes. The directions and points of application of left and right temporalis, lateral pterygoid and masseter-medial pterygoid muscles were measured on a single skull. The magnitudes of the bite forces were arbitrarily chosen. The magnitudes and directions of the minimum condylar force were calculated for a wide range of bite points and bite force directions. The results showed the following.

(1) There was a condylar force for every bite force investigated.

(2) Bite forces parallel to or within twenty degrees of the sagittal plane resulted in small to moderate forces that pushed the condyle against the articular eminence. Bite forces with large medial or lateral components resulted in moderate to large forces which separated condyle and eminence.

(3) Bite forces that had no medial or lateral component resulted in equal forces on w.s. and b.s. condyles. However, the range of variation in their magnitudes and directions was small. When medial or lateral components were introduced, little symmetry was observed and the range of variation was larger.

Hatcher et al. ('86) developed a mechanical and a mathematical model to study loads at the human TMJs during unilateral biting. The mechanical model consisted of a human skull to which left and right synthetic 'muscles' (deep and superficial masseter, medial pterygoid, and anterior and posterior temporalis) were applied according to published anatomical descriptions. Their directions were maintained by attachment to an external frame. Their magnitudes were chosen by the user and measured by muscle force transducers. A bite force transducer replaced the molar teeth of the upper and lower jaws and was used to measure vertical forces at M1, M2 and M3. TMJ transducers replaced the mandibular fossa and the articular eminence on each side to measure the magnitude and direction of the forces on the condyle. Muscle forces were simulated in proportion to the cross sectional areas of the muscles (based on Schumacher's ('61) data), and in proportion to a combination of their cross sectional areas and their relative activity (derived from previously published electromyographic data). The b.s. muscle force was varied.

The points of application of the forces and the directions of the muscles were measured on the mechanical model and incorporated into the mathematical model. Lateral pterygoid was added to the latter. The magnitudes of the bite and joint forces were then calculated. It was assumed that the component of the joint forces perpendicular to the sagittal plane were the same in both condyles in order to reduce the problem to a statically determinate one. A sensitivity analysis was done on the mathematical model by varying the magnitudes, directions and points of application of the muscle forces.

Variation in the results between one model and the other was often considerable, but both showed similar trends.

(1) Occlusal load increased as the bite point shifted posteriorly.

(2) The b.s. condyle bore more force than the w.s.

condyle.

(3) The condylar force was more evenly distributed between w.s. and b.s. condyles, the smaller the contribution of the b.s. muscles.

In a subsequent paper the authors used the mathematical model to examine the effects of bite force direction on the magnitude of the bite force and the magnitude and direction of the joint force (Faulkner _et al_., '87). Muscle force proportions were based on the combined data on cross sectional areas and EMG activity. Unilateral bite forces of varying directions (parallel to the sagittal plane) were applied on each of the molars. The results showed the following.

(1) The b.s. condyle carried approximately twice the force of the w.s. - one-third on the w.s. and two-thirds on the b.s..

(2) The bite force increased by 50% from M1 to M3, given constant muscle activity. Given constant bite force, muscle activity and total joint force were reduced.

(3) The magnitude of the bite force was larger when it was directed upward and forward than when it was directed upward and backward.

(4) Given constant muscle activity, the direction and magnitude of the b.s. condylar force was essentially unaffected by changes in the direction of the bite force, until biting on M3. The effect of the change in moment arm

was greater at M3. The w.s. condylar force showed considerable change, its direction becoming more horizontal with anteriorly directed bite forces.

(5) The force on the b.s. condyle was approximately perpendicular to the articular eminence, while the direction of the w.s. condylar force varied, depending on bite force direction. The w.s. condyle was positioned centrally in the mandibular fossa and acted as a stabilizing pivot which is lightly loaded. The greater share of the force was carried by the b.s. condyle.

2. Bite Forces

Koolstra et al. ('88) developed a model which allowed them to calculate maximum bite forces and corresponding joint forces for bilateral and unilateral biting. The directions and points of application of the muscle forces were determined by dissection, but measured on radiographs of a human skull. The maximum force of each muscle part (eight on each side) was determined using the physiological cross sections of each, measured by CT-scans. Their proportions were determined by their wet weights. The direction of the joint reaction force was taken to be perpendicular to the condylar surface. The activity of the most active muscle relative to others was minimized successively. The maximum bite force was calculated for a number of bite points and bite force directions as well as various mandibular positions. The results showed the following.

(1) The magnitude of the bite force increased as the bite point was moved from the anterior to the posterior teeth. This was especially true when the bite force was directed perpendicular to the occlusal plane, but not necessarily true for other directions.

(2) The largest possible bite forces were found when biting on M2.

(3) The main direction of the maximum bite force was determined by the bite point location, while the patterns of the muscle force use were independent of it. In general almost all of the muscles exerted their maximum forces to generate maximum bite forces.

(4) The orientations of the muscles were more suitable for generating large bite forces perpendicular to the occlusal plane in the molar region than in the incisor region.

(5) The direction of the maximum bite force was more posterior in the incisor region than in the molar region.

(6) Maximum bilateral bite forces could be larger than corresponding unilateral bite forces, but the muscles appeared suitable to generate unilateral almost as efficiently as bilateral bite forces.

(7) The position of the mandible determined the lines of action of the muscles and thus the maximum bite forces

produced.

(8) The magnitude of the joint reaction force was affected by differences in muscle activity patterns, even if they led to almost identical bite forces. The distribution of force over the two joints was also variable. Relatively large joint forces on the b.s. were observed for medially directed maximum bite forces. On the w.s. they were observed for laterally directed maximum bite forces.

Hannam and Wood ('89) used magnetic resonance imaging to determine the directions and cross sectional areas of the masseter and medial pterygoid muscles in 22 human subjects. The magnitude of the muscle force was arbitrarily chosen for the first set of calculations, and then the cross sectional areas of the muscles were taken into account. The points of application of all of the forces were measured on cephalograms and dental casts of the subjects. The magnitudes of vertical forces on the left or right first molar and on the w.s. and b.s. condyles (presumed vertical in the frontal projection) were calculated. The goal of the study was to determine the effect on bite force of craniofacial differences. The results showed the following.

(1) The masseter was usually about 66% larger in cross section than the medial pterygoid. The former was inclined more anteriorly than the latter. The moment arms of the masseter were on average 50% longer than those of the medial pterygoid. The bite forces produced by the masseter were

greater than those produced by the medial pterygoid. Thus, the masseter was a more effective producer of bite force.

(2) When using the masseter alone, a small distractive force was produced at the b.s. condyle and a larger compressive force at the w.s. condyle. Those forces were smaller when the bite point was on the same side as the muscle. When using the medial pterygoid alone, the forces on both condyles were compressive and were smaller on the b.s. condyle. They were also smaller when the bite point was on the same side as the muscle.

(3) There was no association between the mechanical efficiency of the system (measured by bite force) and the sizes of the two muscles. Thus, subjects with similar skeletal features can have large variation in unilateral molar bite force and similar bite forces can be found in subjects with different skeletal features.

3. Muscle Forces

Osborn and Baragar ('85) developed a computer assisted three dimensional model of the jaw, based on linear programming, which predicted the combination of muscles used to produce a given bite force. The directions of twenty-four muscle parts on two sides were measured on a human skull, as were the points of application of the bite and joint forces. The maximum tensions of each muscle part were a compromise between the ratios of the cross sectional areas provided by Schumacher ('61) and the maximum values calculated by Pruim et al. ('80). The direction of the joint force was assumed to be perpendicular to the articular surface of the condyle. The magnitude of the bite force was arbitrarily chosen and several bite points were tested. The computer was used to find the combination of muscle forces that produced a bilateral vertical bite force. The magnitudes of the muscle and joint forces were calculated.

When the joint reaction was minimized the joint force was zero only when the bite forces were less than 13kg for M1 and 4kg for I1. Large muscle forces were used to produce small bite forces in order that the joint reaction force be reduced, that is, the system was not efficient. In addition the pattern of muscle activity had not been recorded in the literature. When the total muscle force was minimized, however, the pattern of muscle activity fitted well with the published data. The model which minimized the joint load was therefore abandoned in preference for the one that minimized the total muscle force.

Based on the behavior of the muscles, Osborn and Baragar ('85) concluded that there are two extreme types of muscles - power muscles, such as the superficial masseter and medial pterygoid, and control muscles, such as the lateral pterygoid and the oblique parts of the temporalis. Power muscles tend to have the longest moment arms, whereas control muscles are in a good position to balance the condyle on the articular eminence. All of the jaw muscles have both power and control functions but, judging from the behavior of the muscles, one function usually predominates. The ripple effect described the recruitment of anterior muscle parts followed by posterior parts. Given the objective function, muscle parts with longer moment arms were more efficient.

Subsequent applications of the model showed that human molar teeth are oriented to maximize their work efficiency (Baragar and Osborn, '87) and that human incisor teeth are oriented to maximize their cutting efficiency (Osborn _et al_., '87).

D. _The Literature - Extinct Hominid Jaw Mechanics_

The masticatory system of extinct hominids has most often been studied for the information it can provide on diets. Although a number of techniques can be used to study hominid diets (Walker, '81), only those which involve the mechanics of the masticatory system are relevant here.

Most research has been focused on one particular group of hominids, the australopithecines, probably because their masticatory systems appear to differ considerably from those of modern humans. Their teeth and jaws are massive in comparison and this has led researchers to believe that they were designed to withstand tremendous masticatory forces. Two general ideas were forwarded regarding their diet - the food required large forces to break it up, or repetitive forces to break it up (Hylander, '79; Walker, '81).

Extinct members of the Genus Homo, on the other hand, present a similar masticatory morphology to modern humans. The evidence suggests that selection for massive jaws and teeth was relaxed with the advent of stone tool making, allowing food to be partially processed outside the mouth, and with the use of fire for cooking. Thus, the diet itself may not have changed, but the way of processing it had.

The present study is not concerned with the actual diets of extinct hominids as much as it is with the way in which a mechanical analysis of their masticatory systems can be used to determine the way in which they broke up their food. Since the way in which food is broken up depends on its physical properties, such a study can help to determine the types of food eaten.

Very few researchers have examined the mechanical attributes of the masticatory systems of extinct hominids. Pilbeam ('72) made some general comments about improved mechanical efficiency in hominids. The hominid face is short from front to back and deep from top to bottom. As a result, the moment arm of the bite force is shorter and that of the temporalis and masseter longer.

DuBrul ('77) likened the differences between the masticatory systems of A. africanus and that of A. boisei to the differences between those of carnivorous and herbivorous mammals. A. africanus leaned toward the carnivorous construct - effort forces moderate, lengths of effort arms relative to resistance arms adequate but not related to any adaptive feature. On the other hand, A. boisei was highly specialized in the direction of extreme herbivory - effort forces massive, effort moment arms lengthened and resistance arms shortened.

Hylander ('79) suggested that in robust australopithecines large twisting moments were produced by the temporalis and masseter muscles, which have a tendency to evert the lower border of the mandible, and the medial pterygoid muscles, which have the opposite effect. Since the relative activity of these muscles is unknown in extinct hominids, the extent of the twisting effect is unknown. However, given the apparently large components of the muscles in the frontal projection and the evidence suggesting that the bite force also had large transverse components, the twisting moments produced by them were also large. The mandible of the robust australopithecine was, according to Hylander, ideally designed to withstand bending, twisting and shearing stresses of unilateral mastication. The corpus was deep to counter sagittal bending loads, it was transversely thick to counter twisting loads about its long axis, and the cross sectional area of its cortical bone was large to withstand direct shearing loads.

Walker ('81) examined the positions of the masticatory muscles on the skull of a robust australopithecine, using the cranium KNM-ER406 and the mandible KNM-ER729, to determine their lines of action. They were similar to the human but the muscle forces produced by the australopithecine were much larger, judging by the area and shape of their attachment sites. In addition, the size of the occlusal surface of the molars was 4 or 5 times larger. Thus, according to Walker, the australopithecine would have had to generate 4 to 5 times the bite force to achieve the same occlusal pressures as humans.

Rak ('83) described in detail the faces of the four australopithecine species - africanus, robustus, boisei, and afarensis. Much of their facial morphology was determined by the retraction of the dental arch toward the joint, and the extension of the sites of origin of the masticatory muscles as far from the joint as possible. These two antagonistic shifts occurred in varying degrees according to the sequence africanus, robustus, and boisei (the most evolved). Thus, according to Rak, the evolution of the australopithecines involved primarily a selection for increased mechanical efficiency in the masticatory system.

Demes and Creel ('88) estimated maximum bite force for a number of extant hominoids and extinct hominids by calculating the product of muscle force and the ratio of effort and resistance arms. The muscle forces were approximated by estimating their cross sectional areas at right angles to their average lines of action. That of the temporalis was taken to be the area of the infratemporal fossa, and that of the masseter was taken to be eighty percent of that of the temporalis.

The authors found that bite force increased with body weight among extant hominoids. Modern humans had relatively small bite forces, while the East African robust australopithecines had relatively high bite forces for their body weights. Further, modern humans and extinct hominids tended to have higher incisor forces relative to molar forces than nonhuman primates. Bite force showed a strong correlation with molar crown area, indicating that occlusal pressure was much the same in all species. The following conclusions were made.

(1) The australopithecine chewing apparatus was adapted to processing large quantities of low-energy food, but also to breaking up small, hard objects.

(2) Early Homo exerted larger bite forces than recent humans, so reduction of bite force was a late trend in hominid evolution.

(3) Higher incisor bite forces relative to molar bite forces in hominids was due to reduction in dental arch length.

(4) The evolution of the hominid facial profile was the result of a combination of high bite forces on the molars and diminished use of the front teeth for food preparation.

White's ('77) study was the most complete. Models of a "gracile" australopithecine (using the cranium STS5 and the mandible SK23), a "robust" australopithecine (using cranium KNM-ER406 and mandible KNM-ER729) and a modern human (using a dried skull) were constructed. The purpose was to relate structure to function in the masticatory systems of extinct and extant hominids. The effect of masticatory forces on the form of the anterior mandibular corpus during evolution was of particular interest.

Each mandible was placed in the position of working functional movement for a unilateral bite on the left side. The left mandibular condyle was placed in the mandibular fossa, the right condyle on the articular eminence and a bolus of plasticine was placed between the molars of the w.s.. Wires representing 7 muscles (anterior and posterior temporalis, masseter, medial pterygoid, and superior and inferior lateral pterygoid) were attached to each specimen, according to their approximate mean lines of action. These were based on previously published anatomical studies of human muscles as well as a personal study of them. The specimens were then radiographed in three mutually perpendicular planes so that the direction and relative magnitude of each muscle (based on the absolute length of the wires) in each plane could be measured. Actual relative magnitudes were calculated using the proportional cross sectional areas of the muscles (based on Schumacher's ('61) data). The values were adjusted for each hominid based on the assumption that the area of the space between the zygomatic arch and the side of the skull reflects the cross sectional area of the temporalis. The direction of the bite force (in three dimensions) was determined from Graf's ('75) data.

From the projections of the forces, White ('77) made the following comparisons.

(1) The anteroposterior and mediolateral components of the superior head of the lateral pterygoid were almost equal in the modern human model. The anteroposterior component was larger in the STS5 model and the mediolateral component was larger in the KNM-ER406 model. Thus for KNM-ER406 this muscle was most effective in controlling lateral motion of the condyle while for STS5 it was more effective in controlling anteroposterior movement.

(2) The lateral component of masseter was roughly equivalent for the three models. The medial component of medial pterygoid was, however, much larger in the recent human model. The resultant of masseter and medial pterygoid was thus more vertical for the australopithecines. The high ramus of the two australopithecine mandibles contributed to that result.

In the sagittal projection the line of action of the masseter was progressively closer to the molar teeth as one went from modern human to STS5 to KNM-ER406. Viewed in the occlusal projection it had the largest anteroposterior component in the modern human model. In the australopithecine models the masseter was more laterally positioned and the medial pterygoid had a large anteroposterior component.

(3) In the sagittal projection the temporalis was more vertical in the australopithecine models than in the modern human model. In the frontal projection both anterior and posterior parts diverged from the midline in the modern human. In STS5 the anterior part was directed medially and the posterior part laterally. In KNM-ER 406 both converged to the midline. In the transverse projection the anterior part of the temporalis was directed laterally in the modern human and had a large anteroposterior component. In the australopithecines it was directed medially and had a smaller anteroposterior component.

White concluded that the masticatory systems of the two australopithecines departed from that of the modern human in a similar way. They maximized the vertical component of force through the tooth row and spread this force across the entire postcanine dentition.

E. The Literature - Hominid Symphyseal Torque

The hominid mandibular symphysis has received some specific attention because of the differences observed between Australopithecus and Homo. Australpithecines in general are characterized by extensive bony buttressing on the lingual aspect while humans lack that buttressing and are characterized by a distinct labial structure - the chin. DuBrul and Sicher ('54) reviewed several theories on the origin of the human chin and concluded that it resulted from adaptations of the skull to upright posture. The skull shortened from front to back and broadened from side to side. One result was that the lateral pterygoid muscles acquired large medial components of force. When these muscles contracted, the halves of the mandible were squeezed together and the chin developed to withstand the resulting stress at the symphysis.

White ('77) used the models which he constructed (described above) to predict the form of the anterior mandibular corpus in hominids. Increased buttressing was required in australopithecines because they maximized vertical force on the cheek teeth, thus increasing the torque at the symphysis. In addition, the temporalis was directed medially and squeezed the halves of the mandible together when it contracted. The pattern was opposite in modern humans. The evidence of African Plio-Pleistocene hominids, which he described in detail, supported his hypothesis.

Hylander ('84) reviewed the hypothetical patterns of stress in the primate mandibular symphysis (Fig. 5).

(1) Symphyseal bending due to medial transverse bending

of the mandibular corpora, caused by medial force components. The labial and lingual aspects of the symphysis experience tensile and compressive stress respectively.

(2) Symphyseal bending due to lateral transverse bending of the mandibular corpora, caused by lateral force components. The labial and lingual aspects of the symphysis experience compressive and tensile stress respectively.

(3) Symphyseal dorsoventral shear caused by the vertical components of the balancing side muscles. The principal strains at the symphysis are directed at an angle to the midsagittal plane in the frontal projection (Fig. 5).

(4) Symphyseal anteroposterior shear due to the tendency for the b.s. temporalis to pull the b.s. corpus posteriorly relative to the w.s.. The principal strains at the symphysis are directed at an angle to the midsagittal plane in the transverse projection (Fig. 5).

(5) Symphyseal bending associated with twisting of the mandibular corpora about their long axes, the lower borders being everted and the alveolar borders inverted. The lower and upper borders of the symphysis experience tensile and compressive stress respectively.

(6) Symphyseal twisting about the transverse axis of the symphysis due to a tendency for the w.s. mandibular corpus to be depressed while the b.s. is elevated (provided the moment of the muscle resultant exceeds that of the joint force on the b.s.). The principal strains at the symphysis

resemble those for dorsoventral shear, but are directed oppositely.

Hylander ('84) measured in vivo bone strain patterns on the labial surface of the symphysis of _Macaca fascicularis_ to determine the patterns of stress, but the technique cannot be applied to hominids. In the present study a mathematical approach was used.

F. The Literature - Position of the TMJ

The position of the TMJ with respect to the dentition varies considerably among mammals and studies have shown that it has several effects on function.

(1) It affects the path of a mandibular tooth during jaw closing.

(2) It affects the lengths of the moment arms of the masticatory muscles as well as that of the bite force.

(3) It affects gape and muscle tension due to stretching.

These effects have usually been studied in the sagittal projection and only one study (Osborn, '87) examined it in hominids. In the following pages some of the contributions in this area are described.

1. The Path of Tooth Closure

Spurrell ('06) compared the jaws of the carnivore with those of the herbivore. In the carnivore the joint was low and the bite point moved anteriorly when the jaws closed (as in scissors). In the herbivore the joint was high and the teeth met simultaneously when the jaws closed. The carnivore arrangement allowed a larger gape between upper and lower teeth, especially at the anterior end of the dentition. The herbivore solved this problem by lengthening its jaw.

Hoshi ('71) defined a "condyle height index" (Fig. 6) and measured it on eighty mandibles of seventy-eight mammalian species. They were divided into two groups - Zoophagous (animal-eating), including the Orders Carnivora, Chiroptera, Insectivora and certain members of Marsupialia; and Phytophagous (plant-eating), including the Orders Ungulata, Rodentia, Lagomorpha, Primates, Proboscidea and certain members of Marsupialia. The first group was characterized by a low condyle and the second by a high condyle. The high condyle gave the path of jaw closure a large horizontal component and increased the vertical component of masseter, compared to the low condyle. Thus a relationship between diet and the path of jaw closure was implied.

Greaves ('74) suggested that the relationship of the position of the TMJ to both lower and upper tooth rows is important. If, as in the herbivore, the distances between the tooth rows and the joint are equal, regardless of whether the joint is above, below, or on the same level as the teeth, they will meet simultaneously along the row. If, as in the carnivore, the distances are not equal or if one tooth row is above and the other below the joint, scissor-like shearing will take place.

In a subsequent paper Greaves ('80) reexamined the position of the joint in those mammals where it was characteristically above the upper tooth row. When the b.s. joint was above the occlusal plane the masseter and medial pterygoid muscles of both sides carried the lower jaw upward and medially, as observed during the chewing stroke. If the joint was below the occlusal plane the muscles had a lateral component of force not seen during normal mastication. Greaves concluded that, at least in selenodont artiodactyls, the muscles of both sides produce the required movement. Further, the jaw can be moved in two different directions by the same muscles, provided the occlusal planes of the two sides differ.

Osborn ('87) demonstrated the effect, on the relationship between upper and lower molars during closing, of different vertical and horizontal positions of the joint. That relationship was most vertical when the joint was low and posteriorly placed, and most horizontal when the joint was high and anteriorly placed. In addition, a high and more anteriorly placed joint reduced the gape and compromised the efficiency of the muscles due to stretching, compared to a low and posteriorly placed one.

The position of the condyle in a selection of nonhuman primates, modern humans, fossil hominids and hominoids was compared. Among the hominids australopithecines had a high and anteriorly placed condyle while H. erectus had a low and posteriorly placed one. Early Homo had a condyle placed lower yet, with the neanderthals exhibiting the most posteriorly placed ones. The condyle of Homo sapiens was more anteriorly placed when compared to the neanderthals, but exhibited a range of variation in height. Osborn suggested that changes in the position of the joint during hominid evolution were related to changes in the diet or in its processing.

2. The Moment Arms of Forces

Maynard Smith and Savage ('59) suggested that in carnivores the temporalis muscle is developed at the expense of the masseter because it best balances the anterior and downward forces of a struggling prey. The mechanical advantage of the muscle is increased by positioning the coronoid process high above the condyle, which in turn is positioned at the level of the tooth row. In herbivores the masseter and pterygoid muscles are more developed since they contribute best to the rotation of the mandible in the transverse plane, a movement required for lateral grinding. The mechanical advantage of the masseter is increased by positioning the mandibular condyle high above the tooth row.

Arendsen de Wolff-Exalto ('51) examined 174 mandibles belonging to four orders of animals - animalivorous (Orders Insectivora and Carnivora) and herbivorous (Orders Rodentia and Artiodactyla). On average the herbivorous forms had a higher condyle than the animalivorous forms. However, the average value for the Order Insectivora was nearly as great as that for the Artiodactyla, and that of the Order Rodentia was nearest to the Carnivora. Members of each group showed a large range of variation. Treating the lower jaw as a lever, the higher the condyle, the smaller the bite force at the molars and the smaller the difference in that bite force between the front and back molars. The effects on the path of jaw closure were also noted.

Ward and Molnar ('80) developed a mechanical system capable of replicating human and nonhuman primate chewing motions. The forces of masseter-medial pterygoid, anterior, middle and oblique temporalis, lateral pterygoid and digastric muscles were represented. The occlusal forces were recorded as photoelastic fringes in a urethane alveolar process containing acrylic models of teeth dipped in silicone resin (to represent the periodontal ligament). Experiments were conducted to test the effects of zygomatic root position, which represented the position of the superficial masseter attachment, and condyle height during a symmetrical mandibular motion.

(1) When the line of action of the masseter was tilted

forward there was an absolute increase in occlusal load on each postcanine tooth, and the gradient of occlusal loads from back to front was less noticeable. When tilted backward the occlusal loads were larger at the back of the dentition. In both cases the loads were greater on the mesial half of a tooth than on the distal half.

(2) When the vertical distance between the mandibular condyle and the occlusal plane was varied, the absolute tooth load increased with increased distance. This was attributed to the increased vertical component of the masseter when the condyle was high. A gradient in occlusal load (the posterior teeth being loaded more than the anterior teeth) appeared for low positions of the condyle, while it virtually disappeared for higher positions. The anteroposterior components of occlusal force increased with increased height of the condyle only if the mandible acted as a pure hinge, otherwise all teeth were loaded approximately parallel to their axial orientation.

The authors suggested that the masticatory systems of the robust australopithecines were designed to distribute high magnitude forces evenly on the postcanine teeth.

3. Gape and Muscle Tension

Herring and Herring ('74) used a model to measure the effect on gape of the position of the joint with respect to the attachment points of the superficial masseter (Fig. 7).

A large gape stretched the muscle and reduced the tension which it could develop. They determined that the stretch in the muscle was smaller the greater the difference between "a" and "b" (shown in Fig. 7). Maximum muscle stretch was produced when a=b. Also, if the origin was lowered or the insertion moved anteriorly stretch was increased (and vice versa). Lengthening "a" or "b" or both increased the length of the muscle and the length of its moment arm. If the lengths of "a" and "b" were held constant, a more obtuse angle ϕ (shown in Fig. 7) lengthened the muscle but shortened its moment arm, while a more acute angle ϕ shortened the muscle and lengthened its moment arm. "a", "b" and the angle ϕ were measured on a variety of mammalian skulls to determine whether each had adapted its superficial masseter to the requirements of a large gape, or to increasing its mechanical advantage.

Carlson ('77) studied the effects of a variable axis of mandibular rotation (translation during rotation) on gape and stretch of the superficial masseter in Macaca mulatta. The measurements (adapted from Herring and Herring, '74) were taken from cephalometric radiographs of eleven adults, with the mandible in three different positions. Translating the mandibular condyle during jaw opening minimized the reduction in torque due to a reduction in moment arm. It also minimized the increase in stretch of the superficial masseter. Thus a better potential for exerting maximum tension during jaw closure was maintained.

G. Summary and Conclusions

Theoretical studies of the human masticatory system using mathematical models have demonstrated that the TMJs are loaded during function, and that the forces - their magnitudes, directions and distribution from w.s. to b.s. - depend on the position, magnitude and direction of both the muscle resultant and the bite force.

The way in which the biomechanics papers were grouped in C. above reflects an important difference between them - the unknowns which were calculated. The fascination with the joint reaction force probably derives from the fact that it cannot be measured in humans and that it has been the subject of debate for at least 70 years. This is not to say that muscle forces and bite forces can be accurately measured, but the methods for estimating them have improved considerably with time. For example, Hannam and Wood's ('89) paper introduced a new technique for determining muscle directions using magnetic resonance imaging. Future research should be focused on developing techniques such as these, so that the attributes of the forces in the masticatory system can be more realistically represented.

All of the jaw modeling studies made contributions to our knowledge of jaw function. However, the following conclusions were drawn.

(1) A model operating in three dimensions, so that unilateral biting can be investigated, represents the living system most realistically.

(2) It is important that the methods for estimating attributes of the system be standardized to facilitate comparisons. For example, the number of muscle parts which are required to depict realistic function should be established and their attachment areas clearly defined, so that their directions and points of application are comparable.

(3) In a complete analysis a model should be tested under a number of force conditions. A range of bite forces should be tested since bite force is probably the most important factor affecting the design and function of the masticatory system, being directly attributed to the diet. The attributes of the muscle forces should also be varied to account for the range in the real system of their magnitudes, directions and points of application (see Throckmorton, '85; Throckmorton and Throckmorton, '85; and Hatcher et al., '86).

(4) The number of subjects in the studies varied from one to 22. Most of the results cannot be considered representative until individual variation can be documented.

In the present study the Osborn and Baragar ('85) model was applied. The goal of the study was to determine whether or not the morphological differences between hominids could be related to differences in the way they broke up food. It was assumed that diet governed the direction of the bite force and that the muscles combined to produce an average force which was directed parallel to that bite force. The directions of the muscle forces were considered a reflection of the morphology of each masticatory system and the way they combined a reflection of the way they broke up food. The Osborn and Baragar model allowed those combinations of muscles to be calculated. The model operates in three dimensions and the attributes of all the forces can be manipulated.

Few researchers have examined the hominid masticatory system from a mechanical point of view. Most have focused on australopithecines. None have applied a mathematical model such as those described in C. above. Such an application is the only solution to understanding how the hominid masticatory system works. Further, a model must be applied to all hominid species if the evolution of the modern form is to be understood. Thus, in the present study a mathematical model was applied to a selection of subjects representing every stage of hominid evolution.

The differences between hominids in the morphology of their mandibular symphyses are often considerable. The part that forces in the masticatory system play in that morphology is well recognized. The application of a mathematical model, however, is the only way in which the effect can be calculated. Thus, in the present study a mathematical model was used to determine the magnitudes and directions of symphyseal torque for the selected hominids.

Studies have shown that the position of the TMJ with respect to the dentition affects a) the relationship of upper and lower teeth during jaw closing, b) the moment arms of muscles and c) bite forces and gape. The variation is probably related to the functional requirements of the diet. A study of the effects on jaw closure of TMJ position in hominids might reveal the directions of the bite forces which they were designed to produce. Thus, in the present study a model of tooth closure was applied to the selected hominids.

CHAPTER 2 MATERIALS AND METHODS

A. The Hominid Sample

The main objective in choosing the specimens for this study was that each stage of hominid evolution be represented. The skulls chosen met two further requirements: they were complete enough to obtain the necessary measurements (or the missing parts could be reconstructed), and they represented adult individuals at the time of death.

The fourteen specimens fell into four categories (Table 1, and last page of thesis). The eight skulls in the first category were complete, the cranium and mandible coming from the same individual. The three skulls of the second category were composite reconstructions, the cranium and mandible belonging to different individuals. The two skulls of the third category were reconstructed on paper, in part by using data from another hominid (KNM-ER1813 was reconstructed in two ways). Finally, the fourth category consisted of a skull measured from published photographs. The specimens were provided by the Departments of Oral Biology, Anatomy and Anthropology at the University of Alberta, and by the Department of Anthropology and Archeology at the University of Saskatchewan.

(1) Indian 1 (Fig. 8) was a prepared dried skull and thus dated to recent times. This individual was presumed to originate in India (Sperber, personal communication).

(2) Indian 2 (Fig. 9) was also a prepared dried skull dating to recent times and was, again, presumed to originate in India.

(3) The Amerindian skull (Fig. 10) was unearthed in Edmonton and dates to historic times. It was presumed by the discoverers to be American Indian, though Caucasian admixture cannot be ruled out since it was a post-contact burial. The calvarium was fragmentary but the parts of the masticatory system were intact.

(4) The Australian Aborigine skull (Fig. 11) was identified by its collector and was, according to records, less than 10,000 years old. The skull cap had been removed postmortem (apparently by a stone tool) but was available for study.

(5) The Bushman skull (Fig. 12) was represented by a plaster cast. No information regarding the specific geographic origin or age of the original specimen was available.

(6) The Skhul V skull (Fig. 13) was represented by a plastic cast. The original was found in Israel and dates to about 40,000 years before the present (Trinkhaus and Smith, '85). It was described by Wolpoff ('80) as transitional *Homo sapiens*, between archaic and early modern forms. The specimen presented postmortem distortion on the left side (McCown and Keith, '39), so the right side was measured.

(7) The La Chapelle-aux-Saints skull (Fig. 14) was

represented by a plaster cast. The original was found in France and dates to about 40,000 years before the present (Wolpoff, '80). Considered a 'classic' Neanderthal, it has often been classified as H.s. neanderthalensis (Campbell, '64). Only the left side was measured. The lateral pterygoid plate was incomplete and was reconstructed with plasticine, using a modern human as a model, before the positions of the attachments of the pterygoid muscles were measured.

(8) Rhodesian Man (Fig. 15) was represented by two plaster casts. The original cranial specimen was found in Zambia and dates to between 125,000 and 200,000 years before the present (Brauer, '84). Bearing many Neanderthal characteristics but being considerably older than the 'classic' Neanderthals of Western Europe, it has often been classified as H.s. rhodesiensis (Campbell, '64). Only the left side was measured and the lateral pterygoid plate was reconstructed before doing so.

The cranium lacked an associated mandible. For the purposes of this study it was matched with the Heidelberg mandible (following Dart, '54). Except for the size of the mandibular condyles, the mandible presented a good fit with the cranium. However, the mandibular ramus was too wide anteroposteriorly. The anterior border was therefore reconstructed by removing in the anteroposterior direction about 0.7cm from near its tip, about 1.2cm from about half way along the border and about 1.4cm behind the dentition (the new border was drawn on the cast using chalk). Only the left side was measured.

(9) Peking Man (Fig. 16) was represented by a plaster cast of Weidenreich's ('43) composite reconstruction of the Choukoutien female skull. The original remains were found in China and date to between 400,000 and 600,000 years before the present (Cybulski, '81). They are classified as H. erectus (Weidenreich, '40). The pterygoid plates of both sides were reconstructed before the specimen was measured.

(10) The African Erectus (Fig. 17) was represented by a plastic cast of the cranium. The original specimen, KNM-ER3733, was found in Kenya and dates to between 1.5 and 1.9 million years before the present (Cybulski, '81). Clear resemblances to the Asian H. erectus resulted in that classification for it (Leakey, '76). The specimen appeared to be distorted on the left side. The right side was measured after the pterygoid plates on that side were reconstructed.

The cranial specimen lacked an associated mandible, so one was reconstructed for it, using one of several possible techniques. The effect of the chosen technique on the results was of interest. First, mandibular coordinates for the muscles were found by giving the muscle vectors the same magnitude and direction as those of Peking Man. The magnitude (length) of the vector had no bearing on the operation of the computer model as it was used in this study. The coordinates were then plotted on graph paper in their natural size and a natural size drawing of a sagittal view of the cranium was superimposed on them. The mandible was drawn in to complete the skull. When the averaged occlusal plane on the graph of the muscle coordinates and that on the drawing were aligned, the positions of the mandibular coordinates of Ta, Mda, Mdp, Plm and Pli (see Table 2 for abbreviations of the muscle parts) were judged to be inappropriate. That of Ta was moved forward (changing its direction by five degrees), those of Mda and Mdp were moved backward (changing their direction by ten degrees) and those of Plm and Pli were moved upward (changing their direction by ten degrees). The length of the vector was maintained and the new coordinates were determined from the graph paper. New x' and z' coordinates were thus obtained while the y' coordinates were not altered.

(11) The Habiline Hominid (Fig. 18) was represented by a plastic cast of the cranium. The original specimen, KNM-ER1813, was found in Kenya and dates to between 1.9 and 2.1 million years before the present (Howell, '78). Disagreement exists as to the classification of this specimen. It has been considered a gracile australopithecine of unknown species (Leakey and Walker, '76), or it has been classified as *H. habilis* (Tobias, '85). The left side of the cranium was distorted, so the

right side was measured. The pterygoid plates and the zygomatic arch were reconstructed before doing so. The form of the latter was modeled on STS5.

The cranial specimen lacked an associated mandible, so one was reconstructed for it, using the technique described above for the African Erectus. Indian 2 was used as a model. The mandibular coordinates for the muscles were found by giving the muscle vectors the same direction and magnitude as those of Indian 2. The coordinates were then plotted on graph paper in their natural size and a natural size drawing of a sagittal view of the cranium was superimposed on them. The mandible was drawn in to complete the skull. When the averaged occlusal plane on the graph of the muscle coordinates and that on the drawing were aligned, the mandibular attachment points were judged to be appropriate. Thus the muscles of these two hominids had the same directions.

(12) The Robust Australopithecine (Fig. 19) was represented by two plastic casts. The original cranial specimen, KNM-ER406, was found in Kenya and dates to about 2.2 million years before the present (Leakey and Leakey, '78). It resembled *A. boisei* from Olduvai and thus has been classified with it (Howell and Coppens, '76). The attachment sites of the muscles were preserved to different degrees from one side of the cranium to the other. The temporalis and masseter muscles were measured on the right

side and the medial and lateral pterygoid muscles were measured on the left side.

The cranial specimen lacked an associated mandible. For the purposes of this study it was matched with the mandibular specimen KNM-ER729 (following White, '77). The mandible presented a good fit with the cranium except the bicondylar breadth was too large. Appropriate adjustments were made in the y' coordinates of the muscle attachments to account for the discrepancy. Only the right side of the mandible was measured. The mandibular condyle was reconstructed, using plasticine. The condyle of the Peninj mandible (FNA1/21) served as a model, since it has also been classified as A. boisei. The actual variation in the mandibular condyle of this species is unknown.

(13) The Habiline Hominid skull (above) was also reconstructed using the Gracile Australopithecine (below) as a model (Fig. 20). The mandibular coordinates for the muscles were found by giving the muscle vectors the same direction and magnitude as those of the Gracile Australopithecine. The coordinates were then plotted on graph paper in their natural size and a natural size drawing of a sagittal view of the cranium was superimposed on them. The mandible was drawn in to complete the skull. When the averaged occlusal plane on the graph of the muscle coordinates and that on the drawing were aligned, the positions of the mandibular coordinates of Ta, Tm and Tp

were judged to be inappropriate. These were moved forward, changing the directions of the muscles by ten degrees but maintaining the length of the vector. The new x' and z' coordinates were determined from the graph paper while the y' coordinates were not altered.

(14) The Gracile Australopithecine (Fig. 21) was represented by two casts. The original cranial specimen, STS5, was found in South Africa and dates to between 2 and 3 million years before the present (White et al., '83). It was classified by Robinson ('54a) as Australopithecus africanus. The preservation of the muscle attachment sites differed from one side to the other. The temporalis muscle was measured on the left side and the masseter, medial pterygoid and lateral pterygoid muscles were measured on the right side.

The cranial specimen lacked an associated mandible. For the purposes of this study it was matched with the mandibular specimen SK23 (following White, '77). The mandible presented a good fit with the cranium except for the bicondylar breadth, which was too small. Appropriate adjustments were made in the y' coordinates of the muscle attachments to account for the discrepancy. The specimen was distorted on the right side, so only the left side was measured.

(15) The Afar Hominid (Fig. 22) was represented by photographs of the composite reconstruction of the Hadar

cranial remains (Kimbel et al., '84). The original fragments were found in Ethiopia and date to between 3 and 4 million years before the present (Aronson et al., '77). The Hadar remains are classified as A. afarensis (Johanson et al., '78). Only the left side was measured, directly from the photographs, and all of the measurements were adjusted to natural size.

Fifteen skulls were included in the present study, two of them being different reconstructions of the same individual. Each stage of hominid evolution was represented by at least one specimen, but none was considered representative of the taxon to which it belonged. They were chosen only for the purposes of comparison. Five recent Homo sapiens were included for a number of reasons.

(1) Osborn and Baragar ('85) drew conclusions regarding the human masticatory system after applying their model to one skull. Those conclusions were tested here by applying the model to a number of skulls.

(2) The opportunity to study normal variation in the species was presented. Such a study is particularly valuable since the extent of variation in the extinct hominids is largely unknown. Species distinctions among them have been based on a number of criteria (Tobias, '85) and it remains to be seen if masticatory function can be included among them.

(3) Measurements were more reliably taken on complete

skulls. The computer solutions for reconstructed skulls were better assessed because what was 'normal' was better appreciated.

B. Producing a Bite Force

For this part of the study the computer assisted three dimensional model of the masticatory system presented by Osborn and Baragar ('85), described above, was applied to the hominid sample. The model was based on linear programming, a mathematical method of minimizing or maximizing a function, known as the objective function, which is a linear combination of the unknowns. The objective function is subject to constraints in the form of linear equalities or inequalities. The objective function in the Osborn and Baragar model minimized the sum of the muscle forces subject to the equations of static equilibrium and two further constraints - the magnitude of each muscle force was less than or equal to the maximum assigned it and the magnitude of the joint force was greater than or equal to zero.

In the present study the computer input consisted of two files.

(1) A file listing a) the three dimensional coordinates of the attachment points on the skull of each muscle part and the point of application of the joint reaction force, b) the coefficients in the objective function for each muscle

and joint force, and c) the maximum tension accorded each muscle part.

(2) A file listing features of the desired bite force - its magnitude, direction and point of application in three dimensions.

1. The Muscle Forces

Five human heads were dissected in order to become familiar with the attachment areas of the four main muscles of mastication. The muscles of each hominid were divided into twelve parts on each side of the head. Abbreviations used to represent these muscle parts throughout the text are presented in Table 2.

The temporalis was divided into anterior, middle and posterior parts by first dividing the superior and inferior boundaries of the cranial attachment area into thirds - from the marginal tubercle to the squamosal suture and from the inferior orbital fissure to the anterior border of the posterior root of the zygomatic arch respectively. Superior and inferior divisions were joined with straight lines (Fig. 23). The mandibular attachment area was divided approximately into thirds as illustrated in Figure 23.

The superficial masseter was divided into anterior and posterior parts by dividing the cranial attachment area approximately in half (Fig. 24). The mandibular attachment area was also divided approximately in half, using the estimated average direction of the muscle fibers as a rough guide for positioning the dividing line (Fig. 24). The deep masseter was divided into anterior and posterior parts in the same fashion.

The cranial attachment area of the anterior part of the medial pterygoid was that part outside the pterygoid fossa, on the maxillary tuberosity and the pyramidal process of the palatine (Fig. 25). The attachment of the posterior part was confined to the pterygoid fossa. The mandibular attachment area of the muscle was divided approximately in half, using the estimated average direction of the muscle fibers as a rough guide for positioning the dividing line (Fig. 25).

The part of the lateral pterygoid muscle which attaches to the infratemporal surface of the sphenoid bone was the superior part (Fig. 26). The part attached to the lateral pterygoid plate was approximately halved, for the middle and inferior parts. The mandibular attachment of the superior part was represented by a point on the anterior border of the articular part of the mandibular condyle, approximately half way between the medial and lateral poles (Fig. 26). The pterygoid fovea was divided approximately in half for the middle and inferior parts.

The attachment areas defined in Figures 23 to 26 were those observed in dissection and were not necessarily equivalent to those of Osborn and Baragar ('85). The subdivision of the areas on the skulls was partly arbitrary. The average direction of the muscle fibers was taken into account but a definition which could be applied consistently was also kept in mind.

A colored point was marked on a removable paper dot and placed approximately on the geometric center of each attachment area. Centroids are used when the distribution of a muscle's fibers within its boundaries is precisely known. Even if this information was available for modern humans, there was no way of acquiring it for the extinct hominids. Further, bony attachment areas of masticatory muscles represent them only in part. The muscles are extensively pinnated and a large number of fibers arise from soft tissue structures. .The centroids are thus positioned in space, adjacent to the bone but not directly on it. For these reasons geometric centers were used. Since the anatomy of the muscles of the extinct hominids is unknown, it was presumed that they were similar in their extent of pinnation as well as in their relative mass. The surface areas of the bony attachments alone indicated that this may not have been true. For example, the australopithecines present large mandibular attachments and small cranial attachments when compared to some of the other hominids, such as Peking Man.

The effective line of action of each muscle part was checked on the skull before the coordinates were measured.

This ensured that the path of a straight line joining the cranial and mandibular attachment points was not obstructed by bone. If the path was obstructed, the attachment point closest to the obstruction was moved along the line of action.

The geometric centers of the cranial and mandibular attachment areas of each muscle part were 'joined', by a mathematical calculation done by the computer, with straight lines. These represented each muscle's line of action.

All coordinates were measured relative to a set of axes determined by three mutually perpendicular planes (Fig 27). After considering a number of ways in which the three dimensional coordinates of the points could be measured - by photograph, by radiograph, by computer - a simple but effective method was developed. All of the methods mentioned, though more 'technical', were dismissed for several reasons.

(1) The attachment areas of the pterygoid muscles on the cranium could not be photographed in the three planes.

(2) The density of the materials of which the fossil casts were composed precluded the use of radiographic techniques (even when copper shot was used to mark the attachment points of the muscles).

(3) Due to the incomplete nature of some of the casts, a digitizer which was modified (by the Department of Mechanical Engineering at the U. of A.) to obtain

coordinates on complete recent human skulls was unable to accomodate them.

The measuring 'tools' used in the present study are illustrated in Figure 28. All measurements were made perpendicular to the table top. Each cranium and mandible was positioned three times to find the x, y and z coordinates of the points, measured to the nearest 0.1cm (Fig. 29). The error due to the nature of the fossil specimens - casts based on often fragmentary originals - was presumed to be comparable for all.

Both sides of the skull were usually measured, to serve as a check on the numbers obtained, but only one side was used. Those coordinates were entered into the computer file and were duplicated for the opposite side. The file was symmetrized to simplify the solutions. The solutions for a bilateral bite were symmetric and those for the unilateral bite were not complicated by left-right differences in muscle moment arms. This was not to deny, however, that those differences existed in life.

The maximum force a muscle can exert is proportional to its physiological cross section (PCS), defined as the sum of the cross sections of its individual fibers (Weber, 1846, in Weijs and Hillen, '84). The PCSs of Weijs and Hillen ('85) were used since they represented recent estimates. They were multiplied by 3.5kg/cm^2 (the maximum force per unit area proposed by Ganong, '75) to obtain a maximum muscle tension for each of the four main muscles. The maxima were multiplied by the ratios of the wet weight of each part of a muscle to that of the whole (Table 3). The absolute values were less important than their ratios.

The maxima differed from those used by Osborn and Baragar ('85). They based their maxima upon those of Pruim et al. ('80), estimated from the PCSs provided by Schumacher ('61) and the integrated EMGs of the muscles of seven subjects taken during symmetric biting. The ratios differed most with respect to the lateral pterygoid muscle (Table 3).

The sizes of the muscles of different hominids differed, judging by the size and morphology of their attachment areas. This suggests that the maximum tensions of the muscles also differed. No reliable technique exists, however, for estimating the size and maximum tension of muscles of extinct hominids. A study of surface areas of muscle attachments and cross sectional areas of temporal fossae was conducted. However, neither technique was effective in estimating muscle size, though some authors have used the latter (White,'77; Demes and Creel, '88). The relationship between the bony attachment area of a muscle and its physiological cross sectional area is unknown, and the temporal foramen can only account for the size of the temporalis and possibly the deep masseter muscle.

The muscle maxima were held constant for all of the hominids so that the differences in the solutions due to differences in the geometry of the muscles were not obscured by those due to differences in the maxima. This was not to deny, however, that they differed in life, either in their absolute values or in their ratios. The muscle forces, joint reaction forces and torques on the mandible may therefore be overestimated or underestimated for different hominids in the present study.

Because the muscles of different hominids were different sizes, the way in which they produced a given bite force may not be comparable. The maxima, and thus the capabilities of the hominids were different. Comparisons for equivalent percentages of their maxima might be more relevant. In the present study, however, they were compared at face value.

Finally, the value of the coefficients in the objective function of the linear programming problem was set at 1.0 for all the muscle forces. This assumed that the 24 muscle parts were equally able to participate in the production of the bite force. For the linear programming problem it meant that the cost per unit tension of using a muscle force was the same for all muscles.

2. The Joint Forces

Only the magnitudes of the joint reaction forces were investigated in the present study. The points of application and the directions of the forces, given different bite reaction forces, has been investigated by Osborn and Baragar (paper submitted for publication).

The point of application of a joint reaction force was the approximate midpoint of the articular surface of the mandibular condyle.

The articulating surfaces of a synovial joint have a very low coefficient of friction, so the joint reaction force must be directed perpendicular to the articulating surface of the mandibular condyle in order for the mandible to be in equilibrium (Osborn and Baragar, '85). That direction was held the same for all of the hominids so that differences between hominids in the geometry of the muscles were not obscured. The direction chosen represented an approximate average of those measured on the hominids: θ =15 degrees, ϕ =170 degrees and β =15 degrees (Fig. 30). The joint reaction force, modeled in the same way as a muscle, was thus directed downward, backward and inward.

Finally, the value of the coefficients in the objective function for the joint reaction forces was set at 0.5. Baragar (personal communication) found that those forces were more evenly distributed over the articular surface of the condyle, over a range of bite force magnitudes, if they were given a value of 0.5 or 1.0 than if they were given a value of 0.1 (as they were in the '85 study). This result was judged to be more likely. For the linear programming problem the joint reaction forces were therefore minimized less than the muscle forces, so it was 'cheaper' to load the joint than to use muscle force.

3. The Bite Force

The point of application of the bite reaction force was the approximate midpoint of the occlusal surface of a mandibular tooth. In this study only three bite points were investigated - the midpoint between the two mandibular central incisors, the midpoint between left and right mandibular first molars (simulating bilateral clenching), and the left first molar.

The direction in three dimensions of the bite force is largely unknown in humans, though some attempt has been made to measure it in vivo (Graf et al., '74). It is necessarily unknown for the extinct hominids and depended on the properties of the food being eaten.

It has been suggested that if the torques on a tooth are to be minimized, the bite force would be directed down the long axis of the tooth (Osborn, personal communication). In the modern human jaw the teeth are tilted forward to a varying degree in the sagittal plane, producing the curve of Spee. Thus a bite force directed forward, rather than backward, was chosen. In the frontal plane they are tilted inward, producing the curve of Monson (Osborn, '81). Because the direction of the long axes of the teeth could not be measured for all of the hominids in the present study, two bite reaction force directions were chosen - perpendicular to the averaged occlusal plane (θ =180, ϕ =0), and twenty degrees forward from the vertical to the averaged occlusal plane (θ =160, ϕ =180).

For each hominid the solution for a range of bite forces from zero to its maximum (no more than 100kg) at 5kg increments was investigated. The maximum bite force depended in part on the maximum muscle force available. Though the absolute values were less important than their ratios, the total was 104.8kg. For a bilateral bite, therefore, the sum of the tensions on each side was 104.8kg.

To summarize this section, the following bites were simulated for each hominid in the present study.

(1) Bilateral bite force directed perpendicular to the occlusal plane on the first molars (M1).

(2) Bilateral bite force directed twenty degrees forward on the first molars.

(3) Bilateral bite force directed perpendicular to the occlusal plane on the central incisors (I1).

(4) Bilateral bite force directed twenty degrees forward on the central incisors.

(5) Unilateral bite force directed perpendicular to the occlusal plane on the left first molar (LM1).

All hominids were given the same muscle force maxima and joint reaction force direction. They differed in the position and directions of their muscle forces, and the positions of their joint reaction and bite reaction forces.

Each computer output predicted a tension for each muscle as well as a joint reaction force. The information was used to calculate bite force efficiency (bite force divided by muscle force).

C. Symphyseal Torque

The information in the computer output was used to calculate torque at the mandibular symphysis of each hominid. The torque caused by a force is the vector product of the position vector of the force and the force. The position vector joins the center of rotation with the point of application of the force.

The direction of the rotation caused by a force is determined by the right hand rule - counterclockwise or clockwise (Fuller et al., '78). Its magnitude is the product of the magnitude of the force and the perpendicular distance from the center of rotation to the line of action of the force.

The resultant torque at the hominid symphysis was the vector sum of the torques caused by all of the forces on one side. The center of rotation, the symphyseal point, was arbitrarily chosen and defined as follows. The x coordinate was that of the canine, the y coordinate was zero and the z coordinate was that of the central incisor less 2cm.

For static equilibrium external torque about the symphyseal point is balanced by an equal and opposite internal torque. For the unilateral bite balancing side forces were used because there were fewer of them.

In the present study symphyseal torque was calculated for each hominid for the following bites.

(1) 40kg bilateral vertical and anterior bites on I1, the maximum value at which there was a solution for every hominid.

(2) 40kg and 50kg bilateral vertical and 50kg anterior bites on M1, for comparative purposes and because there was a solution for every hominid.

(3) 50kg unilateral vertical bite on LM1, for comparative purposes. For two hominids, H1 and GA, there was no solution at 50kg bite force. In these two cases torque was calculated for the maximum bite force.

D. TMJ Position

For this part of the research a model of jaw movement proposed by Osborn and Baragar (unpublished research) was applied to the hominid sample. The working side condyle is firmly seated against the articular eminence during biting (Gibbs and Lundeen, '82). The occlusal surface of a working side tooth can therefore be modeled as a point constrained to move along the surface of a sphere centered at that condyle (Fig. 31).

If a tooth moves parallel to its long axis, and the surface of its crown is perpendicular to it, food is crushed between it and the opposing tooth (Osborn and Lumsden, '78). If the tooth moves in a direction perpendicular to its long axis, food is sheared (Fig. 32). Because a tooth moves on the surface of a sphere there are crushing and shearing components in every closing movement. The maximum crush/shear ratio for a tooth can be found using the geometric relationships illustrated in Figure 33.

In three dimensions the position of a tooth with respect to its condyle was measured in the sagittal plane by h, the height of the condyle and r, the effective ramus width, and in the frontal plane by b, the condyle breadth (Fig. 34). Maximum crush/shear ratios were calculated for two values of K, simulating larger or smaller food particles, for the first molar and for a molar positioned closer to the joint (by subtracting 2cm from r of M1). The tooth surface was modeled as flat, perpendicular to the long axis of the tooth. It was thus represented by a point (Fig. 33), so the crushing component was the z component of the tooth's path and the shearing component was the vector sum of the x and y components. To recognize adaptations for improved crushing and shearing in the hominids, the orientation of the long axes of the teeth must, however, be considered. When a tooth is tilted forward, its crushing capability is improved (Fig. 35). However, the orientation of the teeth could not be measured on all of the hominids.

CHAPTER 3 RESULTS AND DISCUSSION

A. Producing a Bite Force

1. The Directions of the Muscles

The line of action of a muscle was defined by a straight line joining the geometric centers of its cranial and mandibular attachment areas. The coordinates in three dimensions of the muscle attachment points and the bite points are presented in Tables 4 to 18. The direction of each muscle force is expressed as three dimensional components of its unit vector (of length 1) in Table 19. When the x, y and z components were positive, the force was directed forward, outward (on the left side) and upward. When they were negative it was directed backward, inward (on the left side) and downward (Fig. 27).

Only one study (White, '77) exists in which the muscle directions of extinct hominids were measured. The mandibles of the models of STS5/SK23 (the Gracile Australopithecine in the present study) and KNM-ER406/KNM-ER729 (the Robust Australopithecine in the present study) were, however, positioned laterally before the muscle directions were measured. This simulated their line of action before a medially directed bite force. Further, only six parts on each side of the head were specified (there are twelve in the present study) and their attachment points were defined differently. Finally, for the KNM-ER406/KNMER729 model the origin of the temporalis was raised above the surface of the cranium in order to account for the (inferred) bulk of the muscle. Because of these differences in technique, the muscle directions are not directly comparable to those in the present study. Nevertheless, the muscles had similar directions. One notable exception was the anterior part of temporalis in the STS5/SK23 model, directed inward for White and outward in the present study. White combined middle and anterior parts for the anterior temporalis, whereas in the present study Ta and Tm were isolated. He suggested that symphyseal torque in Homo and Australopithecus differed because the direction of Ta differed. Results of the present study do not support those claims (see below).

Different directions for equivalent muscles among the hominids are due to different shapes of their masticatory systems. Different moment arms may be due to differences in shape and size. Only I2 and H2 had the same muscle directions because H2 was modeled on I2 (see Table 19 and p.53 above). GA and H1 had the same muscle directions, except for the temporalis, because H1 was modeled on GA (see p.54). Finally, PM and AE had some muscle directions that were the same because AE was partially modeled on PM (see p.51). However, none of the hominids had the same moment arms for equivalent muscles (Table 20), so the solutions to produce an increasing bite force were different (see below).

The way or ways in which the masticatory systems of two hominids differ is difficult to determine. The direction of a muscle depends on the position of the cranial and mandibular attachment points with respect to each other (Fig. 36). Differences between two hominids can thus be attributed to differences in either or both points in three dimensions. The way in which the attachment points differ affects the length of the moment arm (Fig. 37), so a comparison of moment arms might reveal possible causes for the differences between hominids. For example, if the moment arm of Msa for one hominid is longer than that of another, the attachment points of the first hominid's muscle may be more forward and/or downward. Whether the cranial or the mandibular point is primarily responsible for the difference is unknown. If the x component of the unit vector of the muscle force for the first hominid is large in comparison to the second, then it is more likely that the cranial point is responsible. The first step in such a comparison is to scale the skulls to the same size. In the present study, however, the size of the skulls had no bearing on the analysis of the solutions to produce an increasing bite force, or of crush:shear ratios. Thus, they were not scaled.

In a statistically valid population sample, individuals whose dimensions are more than two standard deviations from the mean form less than 4% of the population. These might, therefore, be considered unusual. The 15 hominids of the present study represent as many as 15 different populations, so the average of any of their measurements is probably meaningless. Still, within the group a measurement more than two standard deviations from the average might be considered unusual. In all of the tables provided, values more than two standard deviations from the mean are indicated by asterisks. Some of them are noted below.

2. The Selection of Muscles

Following a study of bilateral biting using one human skull, Osborn and Baragar ('85) concluded that there were two extreme types of masticatory muscles. Power muscles, such as the superficial masseter and the medial pterygoid, have long moment arms. Control muscles, such as the lateral pterygoid and posterior parts of the temporalis, are in a good position to balance forces which would slide the condyle up or down the articular eminence. These authors suggested that all of the jaw muscles have both power and control functions, but one usually predominates.

All of the solutions for bilateral biting in the present study substantiated Osborn and Baragar's ('85) conclusion. From the solutions for 15 hominids, however, the two types were more closely defined.

Power muscles primarily produced bite force and included all parts of the masseter and medial pterygoid. Their activity for a bilateral bite force was consistent for all of the hominids, regardless of bite force direction or tooth used. With an increasing bite force they were selected according to the length of their moment arms and their components parallel to the chosen bite reaction force. The muscle with the longest moment arm and/or the largest component parallel to the bite reaction force was chosen first. Under certain conditions a muscle with a smaller moment arm was chosen if the component parallel to the bite reaction force was larger. Given the objective function in the linear programming problem, muscles with long moment arms, large components parallel to the bite reaction force and small components causing the condyle to slide on the eminence were more efficient (see below).

A new power muscle was recruited when another had reached its maximum tension (saturated), a parameter introduced into the computer program. It facilitated the interpretation of each solution as well as the comparison of the hominids because the order of decreasing efficiency of muscles was easily observed. In life, however, it is unlikely that one muscle part is used at its maximum tension together with another similarly oriented part at zero tension. The masticatory muscles contain fibers covering a range of directions and having a range of moment arms. As the bite force increased adjacent parts having shorter moment arms but larger components parallel to the bite reaction force might be used.

Control muscles primarily balanced forces on the condyle and included all parts of the temporalis and the lateral pterygoid. Their activity differed for the same problem in different hominids and was usually different for different problems (see next section, p.84). The anterior part of the temporalis (Ta) acted primarily to produce bite force and should perhaps be considered a power muscle. However, it often worked with power muscles before saturating, unlike the masseter and medial pterygoid. Further, for anterior biting it played an important role in balancing (see below). Given the objective function, the most efficient combination of muscles which produced a given bite force depended on the mechanical attributes of the muscles, including the following.

(1) The lengths of their moment arms.

(2) Their components parallel to the bite reaction force.

(3) Their components which caused the condyle to slide up or down the articular eminence.

(4) Their components parallel to the joint reaction force.

For a given resistance arm length the mechanical advantage of the system (power arm:resistance arm) increases with the length of the power arm. The most efficient masticatory muscle, therefore, was the one with the longest moment arm. The moment arms of the muscles (Table 20) were calculated about the origin by the computer.

RA had unusually long moment arms for three of the four parts of masseter. The face of this hominid was large, in both the sagittal and frontal projections, and the cranial attachment point of the masseter was farther forward with respect to the face than in the ottherhominids (Fig. 19). Rak ('83) described A. boisei (the taxon to which this specimen belongs) as most specialized in terms of the advancement of the peripheral face and the retraction of the palate. These changes improved the mechanical advantage of the system during australopithecine evolution.

H1 had unusually short moment arms for Tm and Tp. The cranial attachment was expanded posteriorly when compared to the Gracile Australopithecine (upon which it was modeled, see p.54 above). Tm and Tp were therefore less vertical (Figs. 20 and 21) and their moment arms were shorter.

The moment arms of the hominid muscles could not be directly compared because the skulls were different sizes. When the moment arms were scaled, by setting that of Msa to 10 units (Fig. 38), they were rendered more comparable because they were considered as ratios of the maximum. For all of the hominids the moment arm of Ta fell within the range of the power muscles. Essentially it did function as a power muscle, producing much of the bite force (see next section). The moment arm of Tm was shorter than that of any power muscle except for I1, PM and AH, where it was slightly longer than that of Mdp. For these three hominids it did function as a power muscle and was selected before some power muscles. For H2 and H1 some parts of the lateral pterygoid had longer moment arms than Mdp or Tm, but it never functioned as a power muscle. The moment arms of the power muscles were rarely less than 40% of the maximum whereas the control muscles (except for Ta) were rarely more than 40% of the maximum. A difference between power and control muscles is thus indicated and, if moment arms alone are considered, Ta is a power muscle. However, its function varied with bite force direction (see p.92).

The order of decreasing length of moment arms varied among the hominids as did their proportions of the maximum. Moment arms were the most important attribute in determining a muscle's efficiency, given the objective function. When the difference between the moment arms of two muscles was large, the muscle with the longest moment arm was used. When the difference was small, however, the component parallel to the bite reaction force was important. The decreasing order of moment arms (Fig. 38) does not, therefore, necessarily reflect the order in which the muscles were recruited to produce an increasing bite force.

The differences between the moment arms of different muscle parts also varied among the hominids. For example, there was a large difference for RA between the moment arms of Msa, having the longest, and Mda, having the next longest. This suggests that for this hominid Msa produced large bite forces before recruiting Mda. Similarly Msa for RM, having the longest moment arm, did not produce as large bite forces before Pma, having the next longest moment arm, was recruited. In the present study, however, a power muscle reached saturation before another was recruited, and this does not reflect the living system. Further, as noted above, the solutions indicated that the muscles were not chosen in the order of their moment arms. The bite force at which a muscle was recruited depended on attributes of the other forces in the system.

Only general comparisons of moment arms, therefore, can be made. For example, Pma of RM had a long moment arm compared to the other muscles, and so was more efficient than Pma of the other hominids, which did not exceed their lengths by as much, given similar directions.

Given the same moment arm, when the component parallel to the bite reaction force was larger for one muscle than for another, the first muscle was more efficient (again, given the objective function). The component of the unit vector parallel to the bite reaction force was found by the dot product of the unit vector of each muscle force and the unit vector of each bite reaction force. It was calculated in the sagittal projection because the chosen bite reaction forces had no components in the frontal projection.

Most of the muscle forces had a component parallel to the bite reaction force (Table 21). The exceptions were Pls and Plm for BM, which were directed perpendicular to the vertical bite reaction force, and Pls for AA, which was directed perpendicular to the anterior bite reaction force. These muscles made no contribution to those bite forces. The values were negative for most of the muscles, indicating that they were directed upward while the bite reaction force was directed downward. Some parts of the lateral pterygoid had positive values for some hominids, because they were directed downward.

For temporalis, the component of the unit vector parallel to the vertical bite reaction force was larger than that parallel to the anterior bite reaction force. This suggests that this muscle was more efficient producing vertical bite forces, or balancing vertical components of forces in the system. For AA Ta was directed halfway between the two chosen bite forces, so the component of the unit vector parallel to both was the same.

For masseter and medial pterygoid, the component of the unit vector parallel to the anterior bite reaction force was larger than that parallel to the vertical bite reaction force. This suggests that these muscles were more efficient producing anterior bite forces. The exceptions were Mdp for I1 (which was directed slightly backward), Mdp for PM (the difference was small), and Pma for RA (the difference was also small). At small bite forces, when only masseter and a control muscle were active, the results did indicate that anterior biting was more efficient. However, the anterior bite reaction force required little balancing at the condyle (see below).

As noted above, the component of a muscle force parallel to the bite reaction force was the most important attribute, next to its moment arm, in determining its efficiency. For most of the hominids the component of the unit vector parallel to the vertical bite was largest for Ta (Fig. 39). It often functioned as a power muscle, to produce bite force. For the Gracile Australopithecine the component of the unit vector parallel to the vertical bite was largest for Tm, with the result that Tm was an important power muscle (Fig. 55). For most of the hominids, that component was one of the largest. For some, like I1, PM and AH, Tm was more efficient than some power muscles and functioned as one, producing the bite force (Figs. 42, 50 and 56). A sensitivity analysis of the model would reveal the significance of differences such as these. For example, very small changes in the directions of any of the muscle parts might produce an apparently dramatic change in their activity, especially if their moment arms were affected.

The component of the unit vector parallel to the anterior bite reaction force was largest for Msa or Pma and that for Tm was one of the smallest (Fig. 40). For RA the component parallel to the anterior bite reaction force was especially small for Pmp and it was recruited last

(Fig. 53).

The component of a muscle force which causes the mandibular condyle to slide up or down the articular eminence must be balanced in order to stablize the condyle. The most efficient muscle, therefore, required the least balancing or could be balanced by an efficient muscle. The component of the unit vector which caused the condyle to slide on the eminence (Table 22) was found, in the sagittal projection, by the dot product of the unit vector for each muscle force and the unit vector for a force parallel to the articular surface of the condyle.

The bite reaction force pulled the condyle down the eminence when vertical (the component of the unit vector causing the condyle to slide was -.30), but slightly up the eminence when anterior (.04). This had a noticeable effect on the use of the main balancing muscles (see next section, p.88). Since the joint reaction force was directed perpendicular to the condyle it had no sliding effect.

For all the hominids, the temporalis pulled the condyle up the eminence. For the vertical bite it balanced other muscle forces and the bite reaction force, which pulled the condyle down the eminence. Mda also pulled the condyle up the eminence for some hominids (I1, SV, CS and PM), and Mdp did so for more than half (Fig. 41). The rest of the muscles pulled the condyle down the eminence.

Most of the forces in the system pulled the condyle down the eminence with few muscles able to counteract the slide. If the production of large bite forces is important in the design of the masticatory system, the articular surface of the condyle would not be sloped such that balancing muscles would be exausted well before those producing the bite force. A steeper eminence increases the number of muscles pulling the condyle up, while a flatter eminence decreases the number.

If the masticatory system is designed to produce an efficient bite force (using a minimum of muscle force), then the slope of the articular surface of the condyle conforms to the average direction of the main power producing muscles. When those muscle forces are directed almost perpendicular to the articular surface, then they require little balancing.

The muscles probably respond to the properties of the diet, moving the jaw in a direction which most efficiently breaks it up. The condyle and eminence then remodel in response to the average direction of the muscle forces used. Any change in the diet could render the system less efficient until the remodeling took place. The system probably responds to common items of the diet rather than to rare items requiring extremes in the magnitude and/or direction of forces to break them up. It is more reasonable to suppose that the system is efficient most of the time.

The joint reaction forces had a smaller coefficient in the objective function. Thus it was "cheaper" to load the joint than to use muscle force. For this reason the most efficient muscle should be one nearly parallel to the joint reaction force. Such muscles require less wasteful balancing forces. At the same time, however, that muscle has a large component contributing to the joint reaction force. The component of the unit vector parallel to the joint reaction force was found, in the sagittal projection, by the dot product of the unit vector for each muscle force and the unit vector for the force normal to the articular surface (Table 23).

None of the muscles was directed perpendicular to the joint reaction force. Only one joint reaction force direction was specified for all the hominids. It was suggested above that the condyle remodels so that the joint reaction force is parallel to the average direction of the muscle forces used to break up common items of the diet. A study of actual joint surfaces of the hominids might reveal the relationship, if any, between those forces. Because of the direction chosen for the joint reaction force, the component of the unit vector parallel to the joint reaction force for the power muscles and that for Ta were usually close to one, while that for the control muscles was small.

3. The Computer Solutions

The solutions were determined for increments of 5kg bite force and are indicated by points on the plots (Figs. 42 to 64). These points were joined by a straight line, although intermediate bite forces do not necessarily fall on that line.

a. The Bilateral Bites - Power Muscles

The solutions for the bilateral bites (Figs. 42 to 56) were similar in a number of ways, especially with regard to the activity of the power muscles.

(1) As noted above, the power muscles were recruited for an increasing bite force in an order dictated by the length of the moment arm of the muscle and the component parallel to the bite force.

(2) A power muscle was recruited only when a more efficient muscle reached its maximum tension. There were only two exceptions. One was for the vertical molar bite for SV. Mda was recruited before Pma saturated (Fig. 47). The moment arms of these two muscles were almost identical (Table 20), as were their components of the unit vector parallel to the bite reaction force (Table 21). The difference in their efficiencies, therefore, was very small. Tp was recruited at the same time because Ta had reached its maximum. Mda caused the condyle to slide up the eminence and required less balancing by Tp than Pma, which caused it to slide down the eminence. The computer thus chose to use more of Mda and less of Pma. This behavior

represents the masticatory system more realistically because the two muscles were used together, at less than their maximum tensions (Pruim et al., '80).

The second exception was for the anterior molar bite for CS. Pma and Mda were activated together at 15kg bite force (Fig. 48). In this case Mda functioned in part as a control muscle, balancing the downward pull of Pma on the condyle. Temporalis was recruited later than usual because Mda had a longer moment arm and the component parallel to the bite reaction force was larger.

(3) The tension in the power muscles rose steadily to saturation with an increasing bite force, except for SV and CS (noted above) and PM. For the anterior bite for PM, Pmp saturated at 60kg bite force, then reduced its tension at 65kg, when more of Msp was used. It rose again to saturate at 70kg bite force, when Msp had also reached its maximum tension (Fig. 50). Msp was more efficient because the component of the unit vector parallel to the bite reaction force was larger (Table 21) and the muscle required less balancing than Pmp (Table 22).

(4) All of the power muscles were used at the maximum bite force, unless the balancing muscles were saturated, but not all reached their maximum tension. More often they were all used for the anterior bite, since the temporalis did not saturate at small bite forces and was available for balancing near maximum bite force (see below).

For increasing vertical bite forces the power muscles were recruited in the following way. For the molar bites the recruitment pattern is summarized on p. 96.

(1) Msa was recruited first. It had the longest moment arm and, given the objective function, was the most efficient.

(2) When Msa saturated, Mda and Pma were recruited, at a bite force which depended on the efficiency of the muscles already in use - at this point Msa, Ta and usually Tp. The exceptions were H2 and RA, which used Mda and then Msp (Figs. 52 and 53). Msp was more efficient than Pma for these two hominids because its moment arm was longer (Table 20).

The first of Mda or Pma was recruited for SV, CS, RM, H2 and GA between 25kg and 30kg for the molar bite, and between 20kg and 25kg for the incisor bite. The first was recruited for the remainder of the hominids between 40kg and 45kg for the molar bite, and at 25kg (AE only) and 30kg for the incisor bite. Thus two groups were identified. In Group V.1 (Vertical 1) were early *H. sapiens* (SV, CS and RM). H2 and GA had unique solutions (see p.96). In Group V.2 were the remainder of the hominids - *Australopithecus*, *H. erectus* and recent *H. sapiens*. Msa for the early humans was thus less efficient than in the other hominids - it saturated at smaller bite forces.

(3) When Mda and Pma saturated, Msp was recruited. The

exceptions were again H2 and RA, which recruited Pma next.

For Group V.1, Msp was recruited between 45kg and 50kg for the molar bite, and between 30kg and 35kg for the incisor bite. Msp was not recruited for GA, and for H2 Ta produced the molar bite force between 40kg and 65kg. Msp was recruited for H2 after Ta saturated, followed by Pma at 80kg. For the incisor bite it was recruited for H2 at 50kg. For Group V.2 Msp was recruited between 55kg and 65kg for the molar bite and between 40kg and 55kg for the incisor bite. The muscles were recruited at smaller bite forces for Group V.1 than for Group V2. and so V.1 was less efficient.

(4) When Msp saturated, Mdp and Pmp were recruited. Neither were recruited for AA, H1, GA and AH because they had reached their maximum bite force (Figs. 45, 54, 55 and 56). For Group V.1, the first of Mdp or Pmp was recruited between 55kg and 60kg for the molar bite and between 40kg and 45kg for the incisor bite. For H2 the first was recruited at 90kg and 55kg respectively.

For Group V.2 the first was recruited between 65kg and 75kg for the molar bite, and between 45kg (AE only) and 55kg for the incisor bite. Again, Group V.1 was less efficient since their muscles were recruited at smaller bite forces.

When the bite direction was changed from vertical to anterior (20 degrees forward from the vertical) the following attributes of the system changed.

(1) The mechanical advantage of each muscle declined

because the resistance arm was longer.

(2) For each muscle force the component of the unit vector parallel to the bite reaction force was different (Table 21). For most of the hominids it increased for the power muscles and decreased for the temporalis. It mostly increased for Pls and Plm, and decreased for Pli.

(3) The bite reaction force caused the condyle to slide up rather than down the eminence (see p.82).

Because of these changes in the attributes of the system, the power muscles were not necessarily recruited in the same order for an increasing bite force as they were for the vertical bite. They were also not recruited at the same bite force. The recruitment pattern for the molar bite is summarized on p. 96.

(1) Msa was again recruited first. Given the objective function, its long moment arm rendered it most efficient.

(2) When Msa saturated Mda and Pma were recruited, at a bite force which depended on the efficiency of the muscles already in use - Msa, Ta and sometimes Tp or Pli. The exceptions were I2, H2 and RA, where Msp was recruited after Mda and before Pma. For I2 the component of the unit vector parallel to the anterior bite reaction force for Msp was larger than that for Pma.

For I2, AI, SV, CS, RM, PM, AE and H2 the first of Mda or Pma was recruited between 15kg and (for H2 only) 25kg for the molar bite, and between 10kg (SV only) and 20kg for the incisor bite.

For I1, AA, BM, RA, H1, GA, and AH the first was recruited between 30kg and 35kg for the molar bite, and between 25kg and (for AA only) 30kg for the incisor bite. Two groups were therefore identified. Group A.1 (Anterior 1) included H. erectus, early H. sapiens and some recent H. sapiens (Indian 2 and the Amerindian). Group A.2 included Australopithecus and some recent H. sapiens (Indian 1, the Australian Aborigine and the Bushman). Msa for Group A.1 saturated at smaller bite forces than Group A.2, and thus was less efficient.

(3) When Mda and Pma saturated, Msp was recruited. The exceptions were I2, H2, and RA (noted above), for which Pma was recruited, and PM, for which Pmp was recruited. For PM Pmp was more efficient than Msp because it had a longer moment arm (Table 20).

For Group A.1 Msp was recruited for all, except I2 and H2, between 30kg and 35kg for the molar bite and between 20kg and 25kg for the incisor bite. Pma was recruited instead for I2 at 40kg and for H2 at 50kg for the molar bite, and 30kg and 35kg respectively for the incisor bite.

For Group A.2 Msp was recruited between 40kg (I1 only) and 55kg for the molar bite and between 30kg (I1 only) and (for RA only) 45kg for the incisor bite. Thus the muscles for Group A.1 were recruited at smaller bite forces than Group A.2. Group A.1 was thus more efficient.

(4) When Msp saturated, Mdp and Pmp were recruited. The exception was PM (noted above), for which Msp was recruited.

For Group A.1 the first of Mdp or Pmp was recruited, except for PM and H2 (noted above), between 40kg (CS only) and 55kg for the molar bite, and between 35kg and 45kg for the incisor bite. For the molar bite, Msp was recruited for PM at 60kg and Pmp was recruited for H2 at 65kg. For both of these hominids they were recruited when Ta, working as a power muscle, saturated. For the incisor bite Msp was recruited for PM and Pmp was recruited for H2 at 45kg.

For Group A.2 the first of Mdp or Pmp was recruited between 60kg and 65kg for the molar bite, and between 40kg (H1 only) and 50kg for the incisor bite. Thus, Group A.1 was less efficient than Group A.2, since their muscles were recruited at smaller bite forces.

Two observations were made of the above muscle recruitment patterns.

(1) The bite force at which power muscles were recruited depended on the bite force at which previous ones were saturated. The most efficient power muscle, Msa, thus determined the timing of the recruitment of the others. The bite force at which a power muscle was recruited depended on its efficiency and the efficiencies of those recruited at smaller bite forces. If an equivalent muscle in two hominids was recruited at the same bite force, it did not

necessarily saturate at the same bite force. Groups V.1 and A.1 always recruited and saturated at smaller bite forces than Groups V.2 and A.2. Thus Msa was less efficient and/or some or all of the other power muscles were less efficient.

(2) Early H. sapiens were less efficient than the other hominids for both vertical and anterior bilateral bites. For the anterior bite all early Homo and some recent H. sapiens (I2 and AI) were less efficient than Australopithecus and some other recent H. sapiens (I1, AA and BM). This suggests that some of the hominids may have been designed to produce only certain bite force directions efficiently. The efficiency of H. erectus, I2 and AI dropped for anterior biting, suggesting that these hominids were designed to produce only vertical bites efficiently. Again, the efficiency of certain muscles over others is governed by the objective function. Here the efficiency of a hominid masticatory system was defined by the saturation points of the muscles. The actual efficiencies of muscles and hominids is unknown.

b. The Bilateral Bites - Control Muscles

The activity of the control muscles differed for the vertical and anterior bites. The following was observed for the vertical bite. The recruitment patterns for the molar bite are summarized on p.96.

(1) All of the hominids used Ta either when Msa

saturated (*before* the other power muscles were recruited), or with Msa (in turn *followed* by the other power muscles). Ta mostly produced bite force, it rose steadily to saturation and then it was used at maximum tension up to the maximum bite force.

(2) On the other hand, Tp was the primary balancer, the component of its unit vector preventing the condyle from sliding down the eminence being the largest (Fig. 41). It fluctuated (rising and falling) with an increasing bite force, depending on the balancing needs of the active power muscles. Once reaching its maximum tension it usually did not fall at higher bite forces. Tp was not active for CS (Fig. 48) because the component preventing condyle slide for Ta and Tm was large and most of the power muscles required less balancing. For example, for Msa the component pulling the condyle down the eminence was small and for the deep masseter the component pulling it up was large (Table 22).

(3) Tm usually took over balancing when Tp saturated. The exceptions were for I1 (Fig. 42), SV (Fig. 47), RM (Fig. 49) and PM (Fig. 50), where it was recruited to produce the bite force, *before* Tp saturated. For SV all other power muscles had reached their maximum tension. Given the objective function, for all the hominids Tm was a more efficient muscle for producing bite force than Tp, but for I1, RM and PM the balancing needs of the active power muscles were also smaller. Tm, therefore, was the most

efficient control muscle.

(4) The lateral pterygoid was usually not used during vertical biting. The only exception was for SV, where Pli was used at the maximum bite force. It balanced Tm, which pulled the condyle up the eminence. All power muscles were saturated and Pli was the most efficient control muscle because the component of the unit vector preventing the condyle from sliding up the eminence was the largest (Table 22).

For the anterior bite the activity of the control muscles changed. Their recruitment patterns for the molar bite are summarized on p. 96.

(1) Although Ta continued to produce a significant proportion of the bite force, it played a large part, for most of the hominids, in balancing. It worked with the power muscles, its tension fluctuating for some hominids, before saturating at large bite forces. It rose quickly to saturation at small bite forces for AA, GA and AH only, thus acting primarily as a power muscle.

In contrast to the vertical bite, the anterior bite reaction force required little balancing at the condyle (the component causing condyle slide was .04). Since Ta was more efficient than Tp for producing bite force, it served as both bite force producer and as balancer. Further, some power muscles that had smaller components parallel to the vertical bite force than Ta, now had larger ones (see p.89).

They were now more efficient than Ta and were used at lower bite forces.

(2) Because of the reduced balancing need of the bite reaction force, Tp was used little or not at all. For most of the hominids it balanced Msa at small bite forces or played a part in large bite forces, if Ta had saturated. It was not used at all for I2, AI, SV, CS, PM, and H2.

(3) The behavior of Tm was similar for the vertical and anterior bites. For some hominids it was used to produce bite force while for others it played a part in balancing, when either Ta or Tp had saturated. For a few hominids (SV, CS, H2) it was not used at all.

(4) For most of the hominids the lateral pterygoid was active. For I2, CS and H2 it was used at low bite forces to balance Msa. For these, the component of Msa causing the condyle to slide on the eminence was negligible (Table 22). The resultant of Msa and the bite reaction force pulled it up the eminence only slightly and Pli was the most efficient muscle to balance it. SV came close to a similar solution. The resultant of the two forces pulled the condyle slightly down the eminence. A very small amount of Ta was therefore used to balance it (Fig. 47). For the rest of the hominids Msa had a significant component which caused the condyle to slide up the eminence, and it was therefore balanced by the temporalis.

Judging by their behavior, the control muscles were

Bilateral Vertical Molar Sites: Recruitment of Power Muscles

	SV	CS	RM	I1	I2	AI	AA	BM	PM	AE	RA	H1	AH	H2	GA
1st: Msa 5kg	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
25kg															•
2nd: Mda 25-35kg		•	•											•	
40-45kg				•	•	•		•	•		•	•			
Pma 30kg	•														
40-45kg							•			•			•		•
3rd: Pma 30-40kg		•	•												
45-55kg				•	•	•		•	•			•			
Mda 45-55kg	•						•			•			•		
Msp 55-65kg											•			•	
4th: Msp 45-50kg	•	•	•												
55-70kg				•	•	•	•	•	•	•		•	•		
Pma 70-80kg											•			•	
5th: Mdp 55-60kg	•	•	•												
65-75kg					•	•					•				
Pmp 70-85kg				•				•	•	•				•	
6th: Pmp 60-65kg	•	•	•												
70-85kg					•	•									
Mdp 75-100kg				•				•	•	•				•	

Bilateral Anterior Molar Sites: Recruitment of Power Muscles

	I2	AI	SV	CS	RM	PM	AE	H2	I1	AA	BM	RA	H1	GA	AH
1st: Msa 5kg	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
2nd: Mda 15-20kg	•	•		•	•										
25-30kg								•	•		•	•	•		
Pma 15-20kg			•	•		•	•								
30-35kg									•	•				•	•
3rd: Pma 25-30kg		•			•										
40-55kg											•		•		
Mda 25-30kg			•			•	•								
40-45kg										•				•	•
Msp 25-40kg	•							•				•			
Pmp 30kg						•									
4th: Msp 25-35kg		•	•	•	•		•								
40-55kg									•	•	•		•	•	•
Pma 40-55kg	•							•				•			
5th: Mdp 60kg												•			
Pmp 40-55kg	•	•	•	•	•		•								
60-65kg								•	•	•	•		•	•	•
Msp 60kg						•									
6th: Pmp 65kg												•			
Mdp 50-70kg	•	•		•	•	•	•						•		
75-80kg								•		•	•			•	•

Bilateral Vertical Molar Sites: Recruitment of Control Muscles

	SV	CS	RM	I1	I2	AI	AA	BM	PM	AE	RA	H1	AH	H2	GA
Ta 5kg	•	•				•			•				•	•	•
20-25kg			•	•	•		•	•		•	•	•			
Tm 40-55kg		•		•			•		•		•	•	•		•
60-80kg	•		•		•	•		•		•				•	
Tp 5kg			•	•	•		•	•		•	•	•		•	•
25-45kg	•					•			•				•		
Pli 80kg	•														

Bilateral Anterior Molar Sites: Recruitment of Control Muscles

	I2	AI	SV	CS	RM	PM	AE	H2	I1	AA	BM	RA	H1	GA	AH
Ta 5kg		•	•			•	•							•	•
15-30kg	•			•	•			•	•	•	•	•	•		
Tm 50-60kg					•				•	•		•		•	•
70-75kg	•	•				•	•				•		•		
Tp 5 kg					•		•		•	•	•	•	•		
35-50kg												•	•	•	•
55-75kg								•			•				
Pls 55kg				•											
Plm 50-60kg			•	•											
70-75kg	•	•				•	•		•						
Pli 5kg	•			•				•							
35-45kg	•	•	•	•											
55-75kg					•	•	•	•	•						

5kg Bilateral Vertical Molar Site

	I1	I2	AA	BM	RM	AE	RA	H1	AI	SV	CS	PM	AH	H2	GA
Msa/Tp	•	•	•	•	•	•	•	•							
Msa/Ta									•	•	•	•	•		
Msa/Ta/Tp														•	
Ta/Tp															•

5kg Bilateral Anterior Molar Site

	I1	AA	BM	RM	AE	RA	H1	AI	SV	PM	GA	AH	I2	CS	H2
Msa/Tp	•	•	•	•	•	•	•								
Msa/Ta								•	•	•	•	•			
Msa/Pli													•	•	•

sensitive to changes in bite force direction primarily because the balancing needs of the bite force changed. In the present study the anterior bite force was almost parallel to the joint reaction force. Differences in their behavior might be less noticeable if the bite force was less parallel. Of course the components of the muscles parallel to the bite force were also different, affecting their individual efficiencies. The magnitude of muscle force and thus the magnitude of balancing force required differed.

c. The 5kg Bilateral Bites

One of the differences between the hominids was the first combination of muscles chosen, at 5kg bite force. These results are summarized on p.96. There were primarily two ways in which the power and control muscles combined for vertical biting. For I1, I2, AA, BM, RM, AE, RA and H1 Msa and Tp worked together, Msa exerting the most tension and Tp primarily balancing it. For AI, SV, CS, PM and AH, however, Msa and Ta worked together, Ta exerting the most tension for AI, PM and AH, Msa doing so for CS, and the two exerting equal tensions for SV. A unique solution was found for H2. Msa, Tp and Ta worked together, Msa exerting the most tension followed by Tp and then Ta. A unique solution was also found for GA. Ta worked with Tp, Ta exerting the most tension.

It appeared that it was simply a choice between the two most efficient muscles, Msa and Ta. The moment arms of the muscles, the component of the unit vector parallel to the bite reaction force, the component of the unit vector causing the condyle to slide on the eminence, and the component of the unit vector parallel to the joint reaction force were analyzed. Only the ratios of the moment arms of these two muscles caused the hominids to group as described. For the first group the ratio of the moment arms of Msa/Ta ranged from 1.48-1.76 and for the second group the ratio ranged from 1.30-1.47. For H2 the ratio was 1.94 and for GA it was 1.27.

In general, then, when the moment arms of two muscles were very different (the ratio was large) the one with the longest moment arm was used. If they were less different, the components of the muscles parallel to the bite reaction force were important. There was a point where the muscle with the smaller moment arm (Ta) was more efficient, because it had a larger component parallel to the bite force. This was also true for large bite forces - for some hominids Tm was recruited to produce bite force before power muscles with larger moment arms.

For GA, the moment arms of Msa and Ta were very close, so the muscle for which the component parallel to the bite reaction force was larger (Ta) was used.

For H2 the moment arms of Msa and Ta were very different (the ratio was large) and yet both were used. In this case, however, Ta was not recruited as a power muscle but as a control muscle, to aid Tp in balancing Msa and the bite reaction force. It exerted the least amount of tension of the three muscles. The solution for H2 was unique in another way - the joints were offloaded up to 40kg bite force for a vertical molar bite (Fig. 52). The muscle resultant was parallel to the bite reaction force and passed through the bite point.

When the direction of the bite reaction force was changed to anterior a number of attributes of the system changed and the solutions for an increasing bite force changed (see above). At 5kg bite force, however, the combination of muscles used changed only for I2, CS, H2 and GA. For the first three of these hominids, the resultant of Msa and the anterior bite reaction force pulled the condyle slightly up the eminence, so the lateral pterygoid was used to balance it. For GA, Msa (rather than Tp) and Ta were used together, Ta exerting the most tension.

The differences between the vertical and anterior bites for these four hominids are seen in the closed polygons (Fig. 65) which represent static equilibrium geometrically. Their shapes reflect differences in the shape of the four masticatory systems and their areas reflect the bite force efficiency of each, the smaller area reflecting higher efficiency (less muscle force is expended for the bite force). For GA, again, the moment arms of Msa and Ta were similar and the muscle for which the component parallel to the bite reaction force was larger was used. Ta was used with Tp for the vertical bite and Ta with Msa for the anterior bite.

d. The Incisor Bites

When the bite point was moved from the first molar to the central incisor only one attribute of the system changed - the mechanical advantage of each muscle was reduced because the resistance arm was longer.

The muscle attributes themselves were the same. Thus, only minor differences in the solutions were observed, for the same bite direction, in the way the power muscles were used. They were recruited, though at smaller bite forces, in the same order for an increasing bite force. With regard to the control muscles, the lateral pterygoid made an appearance at maximum vertical bite force in three hominids which had not used it for molar biting. In these cases it balanced Tm, which was recruited to produce the maximum bite force. For SV the tension in Msa exceeded that of Ta at small incisor bite forces, whereas they were equal for the molar bite (Fig. 47). For H2 Ta was not recruited at 5kg incisor bite force, whereas it was for the molar bite (Fig. 52). The polygons for SV and H2 for the vertical bites (Fig. 66) indicate that Msa was used less efficiently and the joint reaction force was increased for the incisor bite.

For H2 there was a reaction force at the joint because, due to the geometry of the system, the muscle resultant could not pass through the bite point. Clearly, the solutions for the hominids for the incisor bite were not proportional to those for the molar bite - they were not exactly the same solutions confined to smaller bite forces.

The differences between the molar and incisor anterior bites involved only the lateral pterygoid muscle and it depended on the balancing needs of each hominid. For I1, for example, it balanced Ta at large molar bite forces, but was not needed for incisor biting because Msp served that function (Fig. 42). For some of the hominids the lateral pterygoid was used at the maximum bite force for the molar bite, but not for the incisor bite, or vice versa. I2 and CS were two of the hominids that used Pli for 5kg molar biting (to balance Msa), but not for incisor biting. Msa was completely balanced by the joint reaction force when biting on the incisors (Figs. 43 and 48).

Finally, the solutions for the hominids did not change in exactly the same way with the change in bite point, because the position of the first molar with respect to the incisors differed. The change in the bite point did, however, have the same general effect, as indicated in the preceeding paragraphs.

e. The Unilateral Bite

When the bite point was moved out of the sagittal plane the following attributes of the system changed.

(1) The mechanical advantage of each b.s. muscle was reduced because each was located farther from the bite point. Given the objective function, the w.s. muscles were therefore more efficient.

(2) Because the w.s. muscles were more efficient than the b.s. muscles, they were used more and, therefore, the resultant was not in the sagittal plane.

(3) Because the muscle resultant was not in the sagittal plane, the joint reaction resultant was not in the sagittal plane - the load on the mandibular condyles was unequal. The position of the joint reaction resultant was determined by the w.s. and b.s. muscles used and their activity.

(4) Because the forces in the system were asymmetric, their medial components did not cancel each other out, as they had for the bilateral bites. Those components had to be balanced in the frontal plane and the selection of muscles was affected.

The y component of the chosen bite reaction force was zero, so the components of the unit vector of the muscles parallel to the bite reaction force were the same as calculated above. The y components of the joint reaction forces, however, were not zero, so the components of the muscles parallel to the joint reaction force were different. Similarly, the muscle forces caused the condyle to slide in the frontal and occlusal projections as well as in the sagittal projection.

The study of bilateral biting uncovered the principles which governed the selection of muscles to produce a bite force, rather than simulated mastication *per se*. Force is usually applied on one side of the mouth at a time. Given the objective function, the mechanical attributes of the muscles governed their selection in producing a unilateral bite as well. The solutions, however, were more complex (Figs. 57 to 64). The recruitment pattern of the muscles is summarized on p.104.

Broad *similarities* between the hominids in the activity of the *power muscles* included the following.

(1) They were not recruited in the same order as they were for the bilateral vertical bites on M1 since their y components now influenced the selection. Msa, however, was still the most efficient power muscle and was recruited first.

(2) For many bite forces they were activated *before* other, more efficient, power muscles on the same side were saturated. Instead, they were activated when a power muscle on the *opposite* side saturated. The order in which muscles were recruited thus often alternated between w.s. and b.s..

(3) The tension in a power muscle often fluctuated with

Unilateral Molar Bite: Recruitment of Working Side Power Muscles

	H1	RA	AM	GA	I2	AA	I1	BM	CS	RM	AI	H2	SV	PM	AE
1st: Msa 5kg	•	•	•		•	•	•	•	•	•	•	•	•	•	•
Pma 5kg				•	•	•									
2nd: Msa 15kg				•											
Pma 20-30kg							•	•			•	•	•	•	•
40kg		•	•												
Mda 25-30kg									•	•					
40kg		•													
3rd: Mda 30-40kg											•	•	•	•	•
Pma 35kg									•						
Pmp 20-40kg				•									•	•	•
45-50kg					•	•	•	•		•					
Msp 45kg										•					
4th: Mda 50-55kg					•		•								
Pmp 40-45kg									•		•				
65kg		•													
Msp 65kg		•													
Mdp 60-65kg		•						•				•			
5th: Msp 50-65kg					•				•		•		•		•
Mdp 50-60kg							•			•				•	
6th: Mdp 50-70kg									•				•		•

Unilateral Molar Bite: Recruitment of Balancing Side Power Muscles

	H2	PM	GA	AM	CS	I1	H1	SV	RM	AA	I2	AI	BM	AE	RA
1st: Msa 5kg			•	•	•	•	•	•	•	•	•	•	•	•	•
25kg		•													
Mda	•														
2nd: Mda 10kg			•												
30-45kg						•	•	•	•	•	•	•	•	•	•
50kg				•											
Pma 25kg					•										
55kg		•													
Msa 25kg	•														
3rd: Msp 45-55kg										•	•	•	•	•	•
60kg	•	•				•									
Mda 30kg					•		•								
60kg		•													
Pma 40-50kg								•	•	•					
Mdp 15kg			•												
40-50kg							•			•					
4th: Pma 60-70kg											•	•	•	•	•
60kg														•	
Msp 20kg			•												
50-55kg								•	•						
Pmp 60kg					•										
5th: Mdp 60-65kg								•	•						
6th: Pmp 70kg								•							

Unilateral Molar Bite: Recruitment of Working Side Control Muscles

	H1	RA	AM	GA	I2	AA	I1	BM	CS	RM	AI	H2	SV	PM	AE
Ta 5kg			•				•	•	•		•		•	•	•
15-30kg	•	•		•	•	•				•		•			
Tm 35-45kg			•			•	•	•	•						
50-60kg		•			•					•	•	•	•	•	•
Tp 5kg	•	•	•	•	•	•	•	•	•	•		•			•
25-35kg											•		•	•	
Pla 65kg									•						
Pli 65-75kg									•				•		

Unilateral Molar Bite: Recruitment of Balancing Side Control Muscles

	H2	PM	GA	AM	CS	I1	H1	SV	RM	AA	I2	AI	BM	AE	RA
Ta 5kg		•	•	•	•		•	•				•			•
20-40kg						•			•	•	•		•		
Tm 25-45kg			•			•	•								
50-75kg		•			•			•		•					•
Tp 5kg	•	•				•			•	•	•		•	•	•
20-30kg				•				•				•			
50-60kg								•	•						
Pli 35kg							•								

an increasing bite force. For bilateral biting the tension in the power muscles rose straight to saturation. Their appearance on the plots thus differed.

(4) Just as for bilateral bites, not all of the power muscles were used at maximum bite force. Their use depended on the availability of balancing forces, in all three directions.

(5) The medial pterygoid on the w.s. and the deep masseter on the b.s. were usually recruited before most other power muscles on the w.s. and b.s. respectively.

The following observations were made of the control muscles.

(1) On the w.s. Ta was an important bite force producer. For many hominids it was recruited first. Its activity resembled that for bilateral vertical biting, always rising quickly to saturation. On the b.s. it was used for many hominids to balance forces on that side. For others it was not used at all. Its activity resembled that for bilateral anterior biting, fluctuating according to the balancing needs of the active power muscles.

(2) Tp was usually an important balancer on the w.s. but was used less, if at all, on the b.s.. Its activity thus resembled its activity during bilateral biting. On the w.s. its activity resembled that for vertical biting and on the b.s. its activity resembled that for anterior biting.

(3) Tm was usually used on the w.s. but, often was not

used on the b.s.. It was used for some hominids to produce bite force and for others it took over the balancing role when Tp saturated. Its activity thus resembled that for bilateral biting. For some hominids Tm functioned as a power muscle during bilateral biting, while for others it functioned as a control muscle.

(4) When all of the parts of the w.s. temporalis saturated, no further bite force could be produced. The b.s. muscles could not produce bite force alone, probably because the resultant force was outside the triangle of support (Fig. 4). The exceptions were H1 (Fig. 62) and GA (Fig. 63). Both of these hominids had aberrant solutions to the production of an increasing unilateral bite force.

(5) The lateral pterygoid played an insignificant role at large bite forces for some hominids (SV, CS and H1).

The way in which the forces in the system were balanced for a 5kg unilateral bite for I1 is seen, in comparison to a bilateral bite, in the closed polygons (Fig. 67).

4. Bite Force Efficiency

Bite force efficiency was found for a selection of bite forces by calculating the ratio of the bite force to the total muscle force (Table 24). Those for the 10kg and 50kg bite forces are illustrated in Figures 68 and 69.

Differences in bite force efficiency between the hominids for a given bite force were caused by a) using different muscles, which necessarily have different attributes and thus different efficiencies, b) using the same muscles having different attributes and/or c) having a different mechanical advantage. One hominid could be more efficient than others at producing one bite force, but less efficient at producing another.

Bite force efficiency decreased with increasing bite force, as more efficient muscles were saturated and less efficient muscles were recruited. It was lower for a given bite force when biting on the incisors because the mechanical advantage of each muscle was reduced. When the bite point was moved out of the sagittal plane, the mechanical advantage of the b.s. muscles was reduced compared to the w.s. muscles. Biting unilaterally, therefore, was usually less efficient, for those bite forces presented in Table 24) than biting bilaterally. For I1 and BM unilateral biting was more efficient than bilateral biting, but only at 10kg bite force.

Bite force efficiency was usually greater, for small bite forces (10kg), when biting anteriorly compared to biting vertically because the bite reaction force required little balancing at the condyle compared to the vertical bite. However, the power muscles were recruited at smaller bite forces because Ta did not contribute as much of the bite force. For larger bite forces, then, it was usually more efficient to bite vertically than anteriorly. The exceptions were, at 50kg molar bite force, AA (where there was no difference), BM and GA.

For CS bite force efficiency for the 40kg and 50kg anterior bites was unusually low (Table 24). The other early H. sapiens, RM and SV, were the next least efficient. These three also had the smallest maximum bite forces (Table 25) and the largest joint reaction forces (Table 26) for the anterior bites. None of the attributes of the muscles were unusual (Tables 20 to 23) but the faces of CS, RM and SV were relatively prognathic, judging by the distance between prosthion and sellion (Fig. 70). On the other hand, the zygomatic tubercle, to which the masseter attached, was relatively close to the joint. Thus the moment arm for the most important power muscle was short, while the moment arm for the bite force was long. Thus, the mechanical advantage of the masticatory system as a whole was small for these hominids.

For most of the bite forces the efficiency of H2 was unusually high (Table 24). Again, none of the attributes of the muscles were unusual (Figs. 20 to 23). H2 was modeled on I2, the next most efficient for most of the bites, but the moment arms of the anterior parts of masseter were longer, so the muscle itself was more efficient, given the objective function. Further, for the bilateral vertical molar bite the joints were offloaded up to 40kg bite force (Fig. 52). H2 had a unique solution such that the resultant of the muscle forces was parallel to the bite reaction force and passed through the bite point (Fig. 66). The unique geometry of this hominid thus resulted in high bite force efficiency.

The curves formed by the plotted efficiencies for the chosen bite forces have similar shapes (Fig. 68 and 69). This suggests that a change in the position or direction of the bite force had a similar effect on each hominid, despite the differences in their morphologies. The implication is that the masticatory systems of the various hominids are broadly similar. An important difference between them, however, is in the distribution of the forces in the frontal projection. Because the bite force had no component in that plane, these differences were not fully revealed.

5. The Maximum Bite Force

The maximum bite force which the hominids produced (Table 25 and Fig. 71) depended on the efficiency of the muscles producing an increasing bite force. Once the control muscles had reached their maximum tension, no further bite force was possible. The maximum bite force was smaller for incisor biting than for molar biting because the mechanical advantage of the muscles was reduced. It was also smaller for unilateral than for bilateral biting because the mechanical advantage of the b.s. muscles was reduced and the b.s. muscles could not produce bite force once the control muscles on the w.s. had saturated.

The maximum anterior bite force was usually smaller than the maximum vertical bite force because the mechanical advantage of the system was reduced and because the power muscles were recruited and saturated at smaller bite forces. For AA, H1, GA and AH, however, the maximum bite force increased when biting anteriorly. The masseter was directed far forward in these hominids, and so was less efficient for biting vertically than anteriorly (Figs. 11, 20, 21, 22 and Table 21). The increase was least for H1. In addition, for AA, GA and AH Tm was recruited before Pmp and Mdp, so the latter were available at larger bite forces.

For CS the maxima for the anterior bites were unusually small (Table 25), but this hominid was unusually inefficient for these bites (noted above). For GA the maxima for the vertical bites were also unusually small (Table 25). The temporalis of this hominid had an unusual direction and it produced most of the bite force. It saturated at smaller bite forces than the other hominids. No further bite force could be produced, despite the availability of power muscles (Fig. 55). The power muscles pulled the condyle down the eminence and no muscle, other than temporalis, was able to prevent it (Table 22).

The range in the maxima for the vertical molar bites was large, with a large standard deviation. When the values for GA are excluded, however, it resembles more closely that for the anterior bites. The maxima reported here depended on the maximum tensions allowed each muscle. Those maxima, and their proportions, may or may not be realistic for the hominids in the present study. For example, the results suggest that Habiline Hominid 2 had a larger maximum bite force (100kg) for the bilateral vertical molar bite than the Robust Australopithecine (75kg). The morphology of the skull of RA, however, suggests that it had well developed muscles, far larger than those of H2. This suggests that RA was capable of much larger bite forces. They were not, however, produced as efficiently as H2.

Finally, because maximum bite force depended on the efficiency of the muscles, the curves formed by the plotted maxima (Fig. 71) resemble those formed by the plotted efficiencies (Figs. 68 and 69).

6. The Joint Reaction Forces

For a given bite force, the magnitudes of the joint reaction forces (Table 26 and Figs. 72 and 73) depended on the mechanical advantage of the muscles used, as well as on their components parallel to the joint reaction force.

The joint reaction force increased with increasing bite force because the magnitude of the muscle force increased and because progressively less efficient muscles were recruited. It was larger for a given bite force when biting on the incisors because the mechanical advantage of all the muscles was reduced. When the bite point was moved out of the sagittal plane, the total joint reaction force usually increased because the mechanical advantage of the b.s. muscles was reduced.

The force on the b.s. condyle was usually larger than that on the w.s. condyle. This result is obtained if w.s. muscles are slightly more active than b.s. muscles, or b.s. muscles are more active (Fig. 4). The exceptions were I1, AI, SV, PM and AE for the 25kg bite force and H2 for the 50kg bite force. The force on the w.s. condyle exceeds that on the b.s. condyle if w.s. muscles are far more active than the b.s. muscles (Fig. 4).

The distribution of the joint reaction forces depended on two factors.

(1) The position of the muscle resultant. That position was determined by the w.s. and b.s. muscles used and their activity.

(2) The shape of the triangle of support, determined by the position of the bite point with respect to the condyles (Fig. 4). Given the position of the muscle resultant in Figure 4, for example, if the bite point was on M3, even more of the load would fall on the b.s. condyle.

The joint reaction force on the w.s. often fluctuated while that on the b.s. usually rose steadily. Occasionally a condyle was offloaded. The w.s. condyle is offloaded if the muscle resultant falls on the line joining the bite point and the b.s. condyle. The b.s. condyle is offloaded if the muscle resultant falls on the line joining the bite point and the w.s. condyle (Fig. 4).

For a given bite force, the joint reaction force was usually larger for the anterior bites than for the vertical bites. The resistance arm was longer and the power muscles were recruited at lower bite forces.

For I2 the joint reaction force was unusually large for the 50kg anterior incisor bite. It was the maximum bite force for this hominid (Table 26) and it was apparent that the masseter had a relatively short moment arm (Fig. 70), making it less efficient. Thus, all muscles were recruited at smaller bite forces (noted above).

For CS the joint reaction force was unusually large for three of the four 50kg bilateral bites. This can be related to its low bite force efficiency. For H2 the joint reaction force was unusually small for the 25kg vertical incisor bite. This can be related to its high bite force efficiency.

H2 was unique in that, up to 40kg bilateral bite force on the first molars, both joints were offloaded (Fig. 52). The only way in which the joints can be offloaded is if the muscle resultant is parallel to the bite reaction force and passes through the bite point. All of the hominids might have been able to offload their joints, at least for small bite forces, by using parts of muscles with lines of action different from those specified in the present study.

For I1 the ratio of w.s. to b.s. forces for the 25kg bite was unusually large (Fig. 73). The w.s. muscles exerted far more tension than the b.s. muscles such that the b.s. condyle was offloaded up to 25kg bite force (Fig. 57). The balancing needs in the frontal plane were minimized by using the almost vertical Ta on the w.s. to produce the majority of the bite force.

For GA the b.s. force for the 25kg bite was unusually large. This was its maximum bite force and the solution for an increasing bite force was aberrant (Fig. 63). It was apparent that the large lateral components of the temporalis and masseter could not be balanced by the small medial components of the medial pterygoid muscle (Fig. 21). CS and RM may have had a similar problem - the medial components in the system were large. This may account in part for the low bite force efficiency of these hominids.

Finally, the curves produced by the plotted joint reaction forces for the bilateral bites were similar (Fig. 72), so the effect of a change in the bite force - either in its direction or its point of application - was similar for all the hominids.

7. Summary and Discussion

The solution to producing a bite force in hominids, given the objective function, depends on all of the attributes of the forces in the masticatory system - their magnitudes, directions and points of application. These attributes in turn reflect the morphology of the masticatory system. Differences in the solutions between hominids thus reflect differences in their morphologies, while similarities in the solutions reflect similarities.

In the present study maximum muscle tensions as well as bite and joint reaction force directions were held constant. In this way any differences or similarities in the bite force solutions could be attributed to the directions of the muscles and/or the points of application of the forces with respect to each other. Only the directions of equivalent muscles could be directly compared because they were independent of skull size. Determining the cause of different directions was, however, a complex three dimensional problem. The differences could be due to the position of one or both attachment points. In the present study the effect of unusual muscle attributes (by definition, with values more than two standard deviations from the mean) on producing a bite force were analyzed.

Only 4 of 15 hominids had some unusual muscle directions, judging by the components of their unit vectors (Table 19), and three of these were reconstructions. These were the Australian Aborigine (AA), Rhodesian Man (RM), the Robust Australopithecine (RA) and the Gracile Australopithecine (GA). For AA the parts of the masseter were directed markedly forward (Fig. 13). The most important consequence was small components parallel to the vertical bite force (Table 21). As a result AA was more efficient during anterior biting than during vertical biting (Table 24).

For RM the parts of the masseter were almost vertical or directed inward (Fig. 15), though they were directed markedly outward in the other hominids. The cranium and mandible were from different individuals and the mandible was inappropriate. Regardless, the effect of components in the frontal plane is significant only for unilateral biting. The solution for RM was not noticeably different from the other hominids (Fig. 60). At low bite forces the muscles recruited were similar to those recruited by other hominids. It was also similar to the solution for bilateral biting (Fig. 49), possibly because the bite force lacked a medial or lateral component.

For RA the middle and posterior parts of the temporalis were directed inward because the hominid had large jaws but a small braincase (Fig. 19). Again, the solution for unilateral biting could be affected, but was not noticeably different from the other hominids (Fig. 63) because the bite force lacked a medial or lateral component.

For GA the middle and posterior parts of the temporalis were more vertical than the other hominids (Fig. 21). The cranial attachment area was small and lacked the posterior expansion seen in Homo, and the morphology of the coronoid process resulted in attachment points placed too close to the joint. Tp was more efficient than usual, having large components parallel to the chosen bite reaction forces (Table 21), and produced most of the bilateral bite force (Fig. 55). The solution for unilateral biting was also aberrant (Fig. 63). The mandible, from a different individual than the cranium, was clearly inappropriate. However, a new reconstruction was not attempted because the results were instructive. White ('77) also reconstructed the Gracile Australopithecine STS5 with the mandible SK23, but his analysis did not reveal the error.

Some of the components of the lateral pterygoid for some hominids were unusual (Table 19). However, the effect of these was not fully revealed because the muscle played only a small role for some hominids in producing anterior bite forces. Some of the power muscles, for example Pma for both RM and RA, also had unusual components (Table 19). Moment arms (Table 20) and components parallel to the bite force (Table 21) were affected, so the efficiency of the muscle was affected. For RA the balancing needs of the muscle also differed from other hominids (Table 22). For both RM and RA Pma was less efficient than some other power muscles, and so was used only for relatively large bite forces (Figs. 49 and 53). Such a result is unlikely because for most of the hominids Pma was an important power muscle.

An error may have existed in the determination or recording of the muscle attachment points for these two hominids (Figs. 15 and 19). Alternatively, an error exists in the reconstruction, since the mandibles of both specimens were not from the same individuals as the crania.

The direction of a muscle affects its moment arm, its components parallel to the bite and joint reaction forces, as well as its component causing the condyle to slide on the eminence. Thus, if a hominid had an unusual muscle direction (x, y or z components were more than two standard deviations from the mean, in Table 19), its other attributes were usually affected (Tables 21 to 23). For some hominids the directions were not unusual by definition, but some of the other attributes were. For example, the lateral pterygoid of SV was directed markedly upward (Fig. 13) and it had an unusually small component pulling the condyle down the eminence (Table 22). For I1 Mdp was directed slightly backward (Fig. 8) and it had an unusually small component parallel to the joint reaction force (Table 23).

Considering the number of muscles incorporated into the analysis, very few had unusual attributes. Thus, it appeared that most of the hominids fell within a certain range of morphological variation. The solutions to produce an increasing bite force were similar in many respects, so the hominids were broadly similar in morphology and function.

Following Osborn and Baragar's ('85) designation, the hominid masticatory muscles were divided into two main functional groups. Power muscles produced the majority of the bite force and included masseter and medial pterygoid. The anterior part of masseter was the most efficient power muscle and the anterior parts of all the power muscles were more efficient than the posterior parts. Thus with an increasing bite force a ripple of muscle activity from front to back was visualized. Control muscles balanced forces which caused the mandibular condyle to slide on the articular eminence and included temporalis and lateral pterygoid. The posterior temporalis (Tp) was the most efficient control muscle, having the largest component preventing the condyle from sliding down the eminence. It was used to a lesser extent during anterior biting. The anterior temporalis (Ta) served both power and control functions. When biting vertically its primary function was to produce bite force. When biting anteriorly it was an important producer of bite force as well as an important balancer. For some hominids Tm produced bite force while in others it took over the balancing function when Tp saturated.

The function of the control muscles was thus more flexible than the power muscles. The primary function of the power muscles was to produce bite force, regardless of bite force direction. On the other hand, the functions of all the control muscles changed with bite force direction. Whereas Ta and Tp were in good positions to be power and control muscles respectively, Tm was in a good position for either power or control functions. For some hominids (such as I1) it functioned as a power muscle, while for others (such as I2) it functioned as a control muscle (Figs. 42 and 43). During hominid evolution the size of the cranial attachment area of the temporalis expanded as the brain increased in size, thus increasing the range of directions of its fibers. The muscle could exert force or balance force over a wider range of directions. This range may have been associated with a more varied diet, since the properties of the diet determine the bite force directions applied to it. This implies that the small-brained australopithecines may have had a less varied diet than the large-brained Homo.

The parts of the lateral pterygoid were particularly variable in their directions and activity. This observation minimizes the controversy concerning it's role in biting which exists among researchers studying its EMG activity. Its variable activity can be explained by its variable morphology. In the present study the lateral pterygoid was not usually used for vertical biting, though it was of some importance for some hominids for anterior biting. The significance of its morphology might be better revealed by different bite reaction and joint reaction force directions.

The lateral pterygoid, along with most of the power muscles, pulled the condyle down the eminence. The temporalis and Mdp were usually the only muscles which could prevent them from doing so (Fig. 41). In life the direction of the joint reaction probably conforms to the average direction of the main power producing muscles which, in turn, conform to the average bite direction required to break up food. If the masseter dominated during chewing then AA would have a steeply sloped condyle in comparison, say, to I2. If Ta dominated it would be nearly flat for most of the hominids. If, however, the direction of the joint force conformed to some average direction between these two or more muscles, it would be more variable, especially in three dimensions.

The most efficient combination of muscles to produce a bite force, given the objective function, depended on a) their moment arms, b) their components parallel to the bite reaction force, c) their components which caused the condyle to slide up or down the eminence, and d) their components parallel to the joint reaction force. The moment arms of the power muscles and Ta were usually more than 40% of that of Msa, while those of the control muscles were usually less than 40%. Moment arms were the most important attribute in determining a muscle's efficiency, but if two muscles had similar moment arms, the one with the largest component parallel to the bite force was recruited first. All of the muscles, excluding some parts of the lateral pterygoid for some hominids, had components parallel to the bite force. Thus in reality both power and control muscles contributed to the bite force. Judging by those components, power muscles, especially Msa and Pma, were more efficient for anterior biting and the temporalis was more efficient for vertical biting.

For bilateral biting the pattern of muscle activity (the order in which the muscles were recruited) was similar for all the hominids. However, the timing of their activity (the bite force at which they were recruited) varied. It depended on the efficiency of the first power muscle recruited (Msa) and the muscles working with it, as well as on the efficiency of each subsequent muscle recruited. For vertical biting the hominids formed two groups. The first group included early H. sapiens - SV, CS and RM - and their power muscles were recruited and saturated at smaller bite forces than the second group. H2 and GA had unique solutions but for the vertical bites fell in the first group. The second group included Australopithecus, H. erectus and recent H. sapiens. Thus early H. sapiens were less efficient than all other hominids. For the anterior bites the hominids again formed two groups. The less efficient group included early H. sapiens and H. erectus, as well as certain recent H. sapiens. The more efficient group included Australopithecus and certain recent

H. sapiens. Some hominids may have been designed to produce certain bite force directions and this implies a certain range in the properties of the diet. H. erectus and certain recent H. sapiens, I2 and AI, were more efficient producing vertical bite forces. Australopithecines were more efficient than early H. sapiens but neither appeared to be designed to produce any particular bite force direction. Their diets may thus have been more varied than that of H. erectus.

When the bite force direction changed from vertical to anterior, the activity of the control muscles was more affected than that of the power muscles. For vertical biting a) Ta acted as a power muscle, producing bite force, b) Tp was the primary balancer, c) Tm usually took over balancing when Tp saturated, and d) lateral pterygoid was not used. On the other hand, for anterior biting a) Ta produced bite force and balanced power muscles, b) Tp was used less, c) Tm was used less, and d) lateral pterygoid was used for some bite forces. The difference was primarily due to the reduced balancing need of the anterior bite reaction force, which was almost parallel to the joint reaction force in the present study.

Two main solutions were chosen to produce the 5kg bilateral bite force. Some hominids used Msa and Tp (see p.96), others used Msa and Ta. The first combination resulted when the moment arm of Msa was more than about one and a half times larger than that of Ta. The second combination resulted when it was no more than about one and a half times larger. The two groupings cut across species boundaries - there were representatives of *Australopithecus*, *H. erectus*, early *H. sapiens* and recent *H. sapiens* in both groups. One combination was not more bite force efficient than the other (Table 24). H2 and GA had unique solutions and for H2 it resulted in no forces at the TMJs.

Except for the effect of reduced mechanical efficiency, muscle activity for incisor biting was very similar to molar biting. The change differed slightly from one hominid to another because the position of the first molar with respect to the incisors differed.

The activity of the muscles for unilateral biting differed considerably from bilateral biting because the forces differed from side to side. The behavior of the temporalis was, to some extent, similar for bilateral and unilateral biting. This might suggest that the temporalis acts predominantly in the sagittal projection. The lateral pterygoid was not used at all. The behavior of the power muscles was dissimilar for the bilateral and unilateral bites, suggesting that most of the activity in the frontal projection concerns the power muscles. The medial pterygoid on the w.s. and the deep masseter on the b.s. were particularly important for unilateral biting, one or more of their parts being recruited at small bite forces, before many other muscle parts.

Bite force efficiency decreased a) with an increasing bite force, b) when biting on the incisors, c) when biting unilaterally, and d) (except for small bite forces) when biting anteriorly (Table 24). Early H. sapiens were unusually inefficient because the mechanical advantage of the system as a whole was poor (Fig. 70).

Bite force efficiency may have been irrelevant during the evolution of the hominid masticatory system. It was assumed that each hominid species was inherently efficient because they survived for long periods of time. Further, the hominid masticatory system was designed to break up food, but if two hominids were designed to break up different foods, then their efficiencies may not be comparable. Scissors and nutcrackers, for example, were also designed to break up objects having different physical properties. However, one would not judge one of them more efficient than the other. Both are efficient in their own right. Finally, except for early H. sapiens, the efficiencies of the hominid species overlap (Tables 24 to 26).

The maximum bite force was smaller a) when biting on the incisors, b) when biting unilaterally, and c) (usually) when biting anteriorly (Table 25). Four hominids - AA, H1, GA and AH - had larger maxima for anterior biting, suggesting that they may have been designed to produce anterior bite forces. For GA and H1, however, the larger maxima for anterior biting may also be due to their unusually small maxima for vertical biting. The size of muscle attachment sites suggest that in life some hominids (such as RA) were able to produce larger bite forces than others (such as H2). However, they may not have produced them as efficiently.

The joint reaction force increased a) with an increasing bite force, b) when biting on the incisors, c) when biting unilaterally, and d) when biting anteriorly (Table 26). For unilateral biting the force on the b.s. condyle was usually larger than that on the w.s. condyle. Because w.s. muscles are usually more active than b.s. muscles (they have a better mechanical advantage), the resultant is on the w.s. of the sagittal plane. However, its exact position in three dimensions, in relation to the bite point, determines w.s. and b.s. condylar force (Fig. 4). The larger force need not necessarily be on the b.s. condyle, as commonly believed (Hylander, '85).

I1 and I2 may have originated from the same geographic population so it was of interest to note the differences between them. I1 (Fig. 8) presented greater facial prognathism than I2 (Fig.9) and the zygomatic bones were relatively far forward (Fig. 70). All of the power muscles were more vertical in I2 and the resistance arm for the molar bite force was relatively short. I2, therefore, produced the vertical bites more efficiently than I1 (Table 24). For I1 Tm was an efficient bite force producer and less lateral pterygoid was required than for I2 for balancing large anterior bite forces. I1, therefore, produced the anterior bites more efficiently than I2 (Table 24). When the timing of power muscle recruitment was analyzed, I1 was again more efficient producing anterior bites than I2. These observations demonstrate that individual variation affects the way in which muscles combine to produce a bite force. Until the range of variation in any hominid population can be determined, hominid species or populations cannot be characterized by their bite force solutions.

Although I1, I2 and AA had some unusual features, neither of the remaining recent H. sapiens (AI and BM) were unusual in any way. Of the five hominids only the computer solutions for AA were notable. AA was more efficient when biting anteriorly than when biting vertically (Fig. 45) because the power muscles were directed far forward (Fig. 11). I1, AA and BM grouped together when the timing of power muscle recruitment for the anterior bite was analyzed. They fell within the more efficient group and were similar in at least one aspect of their morphology. They had low condyles (shallow faces) so their masseters were tilted far forward in comparison to I2 and AI, which had relatively high condyles (deep faces) (Figs. 8 to 12).

In comparison to recent H. sapiens, early H. sapiens (SV, CS, and BM) - were less efficient (Tables 24 to 26). They distinguished themselves as a group, therefore, despite the fact that the shapes of their skulls differed from each other (Figs. 13, 14 and 15). In all three the mechanical advantage of the system was smaller than other hominids (Fig. 70).

Neither of the representatives of H. erectus (PM and AE) had any unusual features. Their efficiencies fell within the range of the modern H. sapiens (Tables 24 to 26 and Figs. 68 and 69). When the timing of power muscle recruitment was analyzed, they grouped with the early H. sapiens for anterior biting, and so were less efficient than other hominids.

AE was modeled on PM so, except for temporalis and deep masseter, their muscle directions were the same. However, the shapes of the skulls differed (Figs. 16 and 17) as did their bite force solutions. For PM Ta was the most efficient muscle and Msa was used with Ta. For AE Msa was the most efficient and Msa was used with Tp (Figs. 50 and 51). AE was more efficient than PM for all bite forces (Table 24). The moment arms of its power muscles were longer and the resistance arms shorter (Fig. 70), so the system as a whole had a greater mechanical advantage.

Habiline Hominid 2 (modeled on I2) was the most bite force efficient of the hominids (Table 24). Habiline Hominid 1 acquired some of the difficulties of its model (GA). The direction of the temporalis was different for H1 and GA, however, so the bite force solutions of H1 were more like the other hominids (Figs. 54 and 55) and H1 was more bite force efficient (Table 24).

Despite the fact that the crania of H2 and H1 were the same, their different muscle directions resulted in markedly different solutions for an increasing bite force. Except for the difficulties with the GA model, both systems appeared to work for this hominid. One cannot speculate, therefore, on which one was more correct. In life the muscles cover a range of directions and these two systems may simply represent two parts of that range.

Except for GA, the solutions for an increasing bite force for the australopithecines were not unusual. Despite the unusual muscle attributes of RA, the efficiencies of RA and AH fell within the range of recent _H. sapiens_ (Tables 24 to 26 and Figs. 68 and 69). The solutions for these two hominids were not notably different from each other. Like AA, AH was more efficient for anterior biting than vertical biting (Fig. 56) because its power muscles were directed far forward (Fig. 22).

Finally, the drawings of the muscle vectors (Figs. 8 to 22) depict the general size and shape of the muscular part of the masticatory systems of the hominids. For example, the skull of AA was long from front to back and shallow from top to bottom when compared to that of AI (Figs. 10 and 11). The early *H.sapiens* and the australopithecines had deep faces compared to the recent *H. sapiens*, resulting in long muscle vectors (Figs. 13, 14 and 15 and 19, 20 and 22). Only the *directions* of those vectors, however, affected the solutions for an increasing bite force.

B. *Symphyseal Torque*

When a muscle of mastication contracts, it applies a force to the mandible which tends to rotate it. The direction of the rotation is determined by the direction and point of application of the force. The torque caused by forces having different directions and points of application with respect to the symphysis can be visualized using Figure 74. The three dimensional components of the torque per unit tension caused by each muscle about the symphyseal point are presented in Table 27.

If the x component of torque was positive it was directed anteriorly. The symphysis was twisted about a horizontal axis such that on the right side the upper border was tensed and the lower border compressed (Fig. 75). The pattern was opposite if the component was negative. For the hominids of the present study the x component was negative for the temporalis, masseter and medial pterygoid muscles. The exceptions were Tp for AE, Ta and Tm for H1, and Mdp for

AH. For these hominids the line of action of the muscle passed above the symphyseal point and was directed outward (see Figs. 17, 20, 22 and 74). For most of the hominids the x component of torque was negative for Pls and Plm and usually negative for Pli. The exceptions were AI and RA. For the joint reaction force, the x component of torque was positive. It was also positive for the bite reaction force when biting on the first molar. When biting on the incisors it was zero since the bite reaction force was in the sagittal plane.

If the y component of torque was positive it was directed medially on the right side and laterally on the left. The symphysis was twisted about a transverse axis such that the upper border was everted and the lower border inverted. The pattern was opposite if the component was negative. For the hominids of the present study it was positive for the muscle forces except for Tp for I2, AA, BM, RM, PM, AE, H2 and AH, for Pls and Plm for RA and for Pli for AA, AE, RA, GA and AH. For the joint reaction force and the molar bite reaction forces the y component was negative. For the vertical incisor bite reaction force it was positive and for the anterior incisor bite reaction force it was negative (except for RM and AH).

If the z component of torque was positive it was directed upward. The symphysis was twisted about a vertical axis such that on the right side the labial surface of the symphysis was compressed and the lingual surface tensed. The pattern was opposite if the component was negative. For the hominids of the present study it was positive for Ta, except for AI, SV, CS, RM, RA and AH. It was positive for Tm, except for CS, RM, RA and AH. It was negative for Tp, except for AE, H1 and GA. The z component was positive for the masseter muscle and negative for the pterygoid muscles. The exceptions were for Pma for SV, H1 and GA, for Pmp for H1 and for Pls for AA, H1 and GA. For the joint reaction force the component was negative and it was negative for the anterior molar bite reaction force. For the other bite reaction forces it was zero.

The calculations of the x, y and z components of torque per unit tension in Table 27 incorporate the directions and positions of the forces in three dimensions, and so are not independent of skull size. Most of the unusual components belonged to the hominids named in the previous sections for unusual muscle attributes. For example, for RM the x components of torque for Msp, Mda and Mdp were unusually large. These same muscles were noted above because they were directed inward rather than outward. For other hominids, such as CS and RA, the unusually large components of torque can be attributed in part to their large size.

The vector sum of the torque at the symphysis was calculated for the right side and is presented in Table 28. For most of the hominids of the present study the x component was negative. Thus the upper border of the symphysis was compressed and the lower border was tensed during biting (Fig. 75). This agrees with Hylander's ('84) experimental results on Macaca fascicularis. The exceptions were H1 for all bites, and GA for the molar bites. For these two hominids the unusual directions of the temporalis, resulting in unusual solutions to produce an increasing bite force, can account for the difference.

For the bilateral bites the y component was zero since the torque caused by muscles of the opposite side balanced it. For the unilateral bite it was negative. Thus the upper border of the symphysis was inverted and the lower border was everted (Fig. 75).

The z component was more variable. For the incisor bites it was more often negative. Thus the labial surface of the symphysis was tensed and the lingual surface compressed. The exceptions were BM, H2, H1 and GA for the vertical bite, and I1, AA, BM, H2, H1 and GA for the anterior bite. For the bilateral vertical bites on the first molar the z component was negative for seven of the hominids. For the anterior bite it was negative for nine and for the unilateral vertical bite it was negative for nine (Table 28).

Once again, the hominids previously noted for unusual attributes had unusual magnitudes of symphyseal torque. For example, early H. sapiens and RA had unusually large torques, while H2 had unusually small ones.

The total torque about the symphysis for the selected bite forces is illustrated in Figure 76. Torque about the symphysis was usually larger when biting on the incisors and when biting anteriorly, because of reduced mechanical advantage. It was usually larger for unilateral biting because of reduced mechanical advantage of the b.s. muscles but also because of the contribution of the y component. Among the least bite force efficient hominids was found the largest torque (CS) and among the most efficient, the smallest (H2). Since the calculation of torque takes into account the size of each jaw, the largest torques were also found among those with the largest jaws (CS, RM and RA) and the smallest among those with the smallest jaws (PM). For the bilateral bites the shape of the plots resemble each other since the change from molar to incisor biting had a similar effect in all the hominids.

White ('77) used three hominid models to represent the large number of specimens which he studied. He did not calculate torques _per se_ but only measured the components of the muscle forces in three planes. White suggested that the anterior part of the temporalis was directed inward for australopithecines, so the halves of the mandible were squeezed together when it contracted. The labial surface of the symphysis was tensed and the lingual surface compressed, and the bony response was lingual buttressing. On the other hand, for Homo the anterior part of the temporalis was directed outward, so the halves of the mandible were pulled apart when it contracted. The labial surface of the symphysis was compressed and the lingual surface tensed, and the bony response was labial buttressing, in the form of the chin.

In the present study the pattern described by White ('77) for australopithecines was found for members of both Australopithecus and Homo. The pattern was therefore not exclusive to the small-brained australopithecines and hominids cannot be characterized in this way. Torque depends on the resultant of a number of muscles used to produce the bite force, the anterior temporalis being only one of them. Only when those muscles and their magnitudes are identified can torque be determined for a given hominid. The characteristics of the other forces in the system must also be known. For example, the direction of the bite force was medial in White's study. Given that same bite force, the computer generated solutions of the present study would differ and so, therefore, would symphyseal torque.

The choice for a hominid between lingual and labial buttressing appears too simple. For a given set of forces one might expect that long jaws need more buttressing than short ones, deep jaws more than shallow ones and wide jaws more than narrow ones. For long, deep or wide jaws the perpendicular distance from the symphyseal point to the point of application of the resultant force is longer, so the magnitude of the torque is larger. Thus torques might be minimized by making the jaws shorter, shallower and narrower.

The symphyseal morphologies of the hominids of the present study were not specifically examined. However, the effect on torque, during unilateral biting, of the position of the symphyseal point, given the forces computed for each, was investigated. For each hominid torque was calculated for four different positions of the symphyseal point. It was moved [illegible] cm a) forward, b) backward, c) downward, and d) upward with respect to its original position. The results indicated the following.

(1) When the symphyseal point was moved forward a) the x component of the total torque was unchanged, b) the y component was smaller (and for H2 and H1 it changed direction), c) the z component was larger for all except I1, I2 and SV, and d) the total torque was smaller except for RM, RA, H1 and GA. When the symphyseal point was moved backward the opposite result was found except the direction of the y component did not change for H2 and H1 and the total for RA was larger.

(2) When the symphyseal point was moved downward a) the x component of the total torque was larger for AI, CS, RM, PM, RA, H1, GA and AH and smaller for I1, I2, AA, BM, SV, AE and H2, b) the y component was larger for SV, PM, H2

and GA and smaller for the other hominids, c) the z component was unchanged, and d) the total torque was larger for the first group in a) and smaller for the second group. When the symphyseal point was moved upward the opposite result was found.

The initial expectation concerning jaw size and torque was thus too simple. For most of the hominids total torque actually decreased when the jaw was lengthened and there was an almost equal split of the hominids when the jaw was deepened. The effect of changing the position of the symphyseal point clearly depended on the direction and point of application of the resultant force. The effect caused by the change in position of the symphyseal point cut across species boundaries, so hominid species could not be characterized in that way.

C. TMJ Position

The position of a mandibular molar with respect to the TMJ governs the path of that tooth during jaw closing. As h decreases and as r and b increase, the vertical component of the path of closure increases with respect to the horizontal or transverse components (Fig. 77), and the ratio of crush:shear is increased.

Given the definition of crushing and shearing, the mandibular tooth was modeled in the present study with a flat surface. If cusps were intact, some crushing would take place beween cusp surfaces during shearing movements of the tooth and some shearing would take place between cusp surfaces during crushing movements of the tooth. The ways in which different foods can be broken up by using different tooth designs have been examined by Lumsden and Osborn ('77), Osborn and Lumsden ('78), Lucas ('79, '82) and Luke and Lucas ('83).

Pure crush and pure shear cannot be achieved, according to the model, because the tooth moves on the surface of a sphere. Pure crush could be achieved if the tooth moves outward and backward (ϕ equals zero). However, during normal mastication it moves upward and inward (Hiiemae, '78). Pure shear could be achieved if pure rotation around the vertical axis was possible (θ equals zero).

Both crushing (vertical) and shearing (horizontal and/or transverse) forces are required to break up food because food must be retained and/or compressed in order to be efficiently divided (Osborn and Lumsden, '78). The ratio of the two forces required to break up a particular food depends on the properties of that food (Lucas and Luke, '84). The properties of an unknown diet might therefore be determined by exploring the crushing and shearing capabilities of the masticatory system.

The ratios of crush:shear required to break up specific foods are unknown. For hominids with flat tooth surfaces, for example, hard brittle items such as nuts or bone would be best broken up by applying predominantly vertical forces (crushing). Fibrous foods such as leaves or meat would be best broken up by applying predominantly horizontal and/or transverse forces (shearing). Some workers have suggested that gracile australopithecines were carnivorous and robust australopithecines were herbivorous (Robinson, '54b). It is apparent, however, that only the *properties* of the food were important, regardless of whether the diet was animal or vegetable. The greater proportion of the diet of every hominid was vegetable - only those proportions changed with time (Gordon, '87).

The maximum crush:shear ratios were, as expected, larger for smaller values of K, because $\delta\phi$ was smaller (Table 29). Thus, the smaller the food particle, the more effective the crush. They were also smaller for the M1-2cm position because r was smaller (Fig. 77). Since the numbers are ratios, the differences between the hominids were not due to differences in the dimensions of their skulls. Only CS had unusually large maximum crush:shear ratios. This hominid had one of the largest values of r and the smallest values of h (Table 29).

The positions of the TMJs in the hominids are plotted in Figure 78 in three projections order to enable the reader to visualize the paths of tooth closure. The largest maximum crush:shear ratios are illustrated in Figure 79.

The crushing component was always greater than the shearing component in the hominids because the TMJ was positioned above the tooth row. Ratios over two, where the component of crush was twice that of shear, were found only for Homo. Australopithecus had ratios less than two. The smallest ratios were thus found for the australopithecines. The largest were found for early Homo, especially Peking Man and the La Chapelle-aux-Saints Hominid. Both of these hominids had low condyles. It was positioned closer to the first molar for PM. These results agree in general with those of Osborn ('87), working in two dimensions.

Because the values reported in Table 26 are maxima, a range of crush:shear ratios below these values were possible and the capabilities of the hominids overlapped. However, the data suggest that the primary elements of the australopithecine diet may have had different properties from those of the early Homo diet. The modern humans showed a range of variation in their ratios, some near those of the australopithecines but none near the maximum value presented by CS. I1 and I2, possibly representing the same population, had quite different ratios.

Finally, the calculations of maximum crush:shear ratios in the present study assumed that the teeth were set vertically in the jaws and that the surface of the tooth was parallel to the x axis of the coordinate system. If a molar tooth is tilted forward as well as inward with respect to the vertical (more parallel to the path of closure), the ratio of crush:shear is considerably improved (Fig. 35). In modern humans the posterior molars are tilted forward and inward, producing the Curve of Spee, so the maximum crush:shear ratios are larger than those calculated here. The orientation of the teeth in the jaws of the hominids could not be determined. It might be measured by the orientation of their occlusal surfaces, provided they are perpendicular to the long axes of the teeth. However, the assumption is valid only if the crown is markedly flattened.

CHAPTER 4 CONCLUSIONS

For some time now anthroplogists have been impressed by the apparently large differences between the masticatory systems of australopithecines and humans. Because the most important function of the masticatory system is to break up food, the differences have been quite naturally attributed to differences in diet. Indecision exists, however, as to the nature of the differences. Were australopithecines eating different food (food having different properties), different quantities of the same food, and/or were they processing food differently?

Because the break up of food by the masticatory system is a purely mechanical process, a mechanical approach is most appropriate for revealing differences between masticatory systems. In the present study a mechanical analysis of the hominid masticatory system was undertaken to reveal possible differences in the way food was broken up, and thus possible differences in diet.

The hominid masticatory system was explored in three ways.

(1) Most of the research concerned the application of a mathematical computer assisted model of the jaw to each hominid. The model predicted the combination of muscles used to produce an efficient bite force. If different combinations were used, then food was broken up differently. Further, the bite force direction that a hominid produced

most efficiently probably reflected the best way to break up its diet.

(2) The results obtained from applying the computer assisted model allowed the torque at the mandibular symphysis to be calculated. The shape of the symphyseal region was probably related to the torques which it was required to resist.

(3) Finally, a model of jaw closure was applied to each hominid and maximum crush:shear ratios calculated for the first molar. Because food having different properties requires different ratios of crush:shear to break it up, potential crush:shear capabilities of the hominids would reflect the properties of their diets.

The results led to the following conclusions.

(1) The results from the computer assisted model indicated that the masticatory systems of the hominids are broadly similar, suggesting that their diets were broadly similar. A limited range of variation was tolerated before efficiency was compromised. At one extreme of that range were early *H. sapiens*. They had small maximum bite forces, large joint loads and low bite force efficiency. Outside of the range of variation the system was very inefficient. GA fell into this category. The solutions for an increasing bite force were aberrant, especially for unilateral biting.

The evidence to support the above conclusion includes the following..

(a) The patterns of muscle recruitment for an increasing bite force were similar for all the hominids. When the point of application or the direction of the bite force was changed, the effects on the activity of the muscles and bite force efficiency (the ratio of bite force to total muscle force) were similar.

(b) Only four hominids of the fifteen had a few unusual muscle directions. It appears, then, that the hominid masticatory system meets certain morphological criteria in its design.

(2) The hominids of different taxa could not be distinguished by the mechanics of their masticatory systems, suggesting that the diets of Australopithecus species and Homo species were similar. The evidence to support this conclusion includes the following.

(a) The activity of the muscles used to produce an increasing bite force cut across taxonomic boundaries. For example, the muscles combined in only two ways to produce a 5kg bite force. Some Australopithecus, H. erectus and H. sapiens used both combinations, indicating similarities, rather than differences, in their morphology and function.

(b) Bite force efficiency, with the possible exception of some early H. sapiens, cut across taxonomic boundaries. The hominids did form two groups when the bite force at which power muscles were recruited was analyzed. However, they could also be grouped in other ways and it is not implied that the groupings are natural. Actual bite force efficiencies of the hominids are unknown.

Australopithecus and early Homo appeared distinct in one respect - early Homo appeared to be adapted for vertical biting. Early H. sapiens and H. erectus were less efficient than the other hominids during anterior biting, when the recruitment of the power muscles was considered. Further, CS, an early H. sapiens and PM, classified as H. erectus, had the largest maximum crush:shear ratios of the hominids.

(c) The patterns of symphyseal torque cut across taxonomic boundaries. For example, some Australopithecus and some Homo had the same patterns.

(d) The maximum crush:shear ratios for the hominids cut across taxonomic boundaries, though some early Homo were at one extreme of the range and some Australopithecus were at the other extreme.

No definitive differences were thus found for any of the hominids and, as a result, no evolutionary trends could be identified in the sample. However, only small improvements over the four million years of hominid evolution might be expected, rather than any major change, and these would not be easily detected.

(3) The components of muscle forces parallel to the bite force appeared to be as important as their moment arms in determining their efficiency. Thus the evolution of the hominid masticatory system was not solely concerned with

improving muscle moment arms, as anthropologists have previously suggested. Nature probably also selected, for each hominid, muscle directions which enabled it to produce a particular range of bite force directions most efficiently. That range depended on the properties of the diet and might be revealed by finding the bite force directions for which each was most efficient.

Moment arms were not specifically explored in the present study. Given certain directions of muscle forces, however, moment arms could substantially change bite force efficiency. For example, H2 was more efficient than I2, although it had the same muscle directions. The moment arms of the important power producing muscles differed however. Similarly, given certain moment arms, the directions of muscle forces are important. If bite force efficiency was important during hominid evolution, long moment arms and large components parallel to the bite force for power producing muscles would have been selected.

The anterior part of superficial masseter and the anterior part of the temporalis were the most important producers of bite force. The most important morphological differences between the masticatory systems of the hominids may therefore lie in the sites of their attachment.

Because the masseter was the most important power muscle, and determined the pattern in which subsequent muscles were recruited, its direction may provide the best clue to the diet of hominids. For example, the diet of the Australian Aborigine may have had different properties from that of Indian 2, since the masseter was directed far forward.

(4) Symphyseal torque can only be determined if the attributes of all the forces in the system are known. The patterns of torque varied among the hominids although Australopithecus could not be distinguished from Homo. Thus the results of the present study oppose White's ('77) conclusions.

(5) Given the results of the analysis of crush:shear ratios, all of the hominids were capable of breaking up a variety of foods. The ranges in the maximum crush:shear ratios for the various hominids overlapped, indicating perhaps that the range in the properties of their diets also overlapped. The most important difference between their diets may have been the proportions of the various food types eaten. Apparently large differences at the extremes of the maxima may indicate some differences in the diets of early H. sapiens and Australopithecus, but these may only reflect individual variation.

That the hominids are broadly similar and thus had broadly similar diets is indicated. There were, of course, differences between them, but these were not judged to be significant, given the following conditions.

(1) The range of variation in the hominids - either

extinct or extant - is unknown.

(2) A sensitivity analysis of both models has yet to be done. The effect on the results of small changes in the attributes of the system, for example muscle directions or positions of the TMJ, is unknown.

In the present study, significance was measured by the range found in the five recent humans. If the results for the extinct forms fell within the range shown by the recent forms, then the differences between them were not judged to be significant. With the possible exception of some early _H. sapiens_ (and H2), muscle activity, bite force efficiency, symphyseal torque and maximum crush:shear ratios fell within the range of the five recent humans.

An important point to be made is that the conclusions are acceptable given the parameters of the present study. When represented more accurately, different results might be obtained and different conclusions might be drawn.

Two additional conclusions were drawn from the results of the present study.

(1) Bilateral biting is unrealistic and, because the bite forces lacked medial or lateral components, revealed more similarities than differences between the hominids. The solutions for the unilateral bite explored here suggested that the hominids were most variable in the frontal projection. For some hominids (CS, RM and RA for example) the components of the pterygoid and temporalis

muscles in the frontal projection were large, implying that bite forces with medial or lateral components were important. If the forces could not be balanced in the frontal projection, the efficiency of the bite force was severely compromised, for example in GA. Comparing hominids in the sagittal projection will not, therefore, necessarily reveal all of the important differences or similarities between them.

(2) The mandible SK23 was inappropriate for the cranium, STS5 (the Gracile Australopithecine). The coronoid process was far too close to the side of the skull, resulting in a temporalis directed markedly outward for GA. Even the temporalis of the large-brained hominids did not have the extreme lateral components of this hominid. The mandible was robust and a simple compensation for a discrepancy in the bicondylar breadth did not improve its fit with the cranium. The coronoid process was ill-matched from front to back as well. The mandible appeared to belong to a hominid with a well developed posterior temporalis. The posterior aspect of the coronoid process was well developed and the semilunar notch was small. As a result, the mandibular attachment points for the parts of the temporalis were too close to the joint. The temporalis was more vertical than in the other hominids, and the solutions for producing a bite force were aberrant. However, when those directions were altered for H1, modeled on GA, the

activity of the muscle more closely resembled that of the other hominids.

Similarly, the Heidelberg mandible was inappropriate for Rhodesian Man. It is unlikely that the masseter for RM was directed inward, as the reconstruction suggested, because it was directed outward for all of the other hominids. This does not deny that some fibers of the masseter may be directed inward in hominids. The masseter is extensively pinnated and muscle fibers arise from soft tissue structures within its mass. The muscle had considerable bulk in the frontal plane in at least one of the individuals which were dissected at the beginning of the study.

Finally, when AE, H2 and H1 were reconstructed by setting their muscle directions according to those of other hominids, they simply acquired many of the characteristics of those hominids. The technique thus had limited value for determining the mechanical attributes of the African *H. erectus* or the Habiline Hominid. For these two, constructing a model of a mandible and measuring the muscle directions on the model is probably just as, or more, appropriate.

The goal of the present study was to determine whether or not the morphological differences between various extinct and extant hominids could be related to mechanical differences in the way they broke up food. That goal was fully realized. Morphological differences between the masticatory systems were reflected in the mechanical attributes of the forces within them, and thus in different efficiencies with which the hominids produced a bite force. Patterns of symphyseal torque, as well as maximum crush:shear ratios also differed. Clearly, the hominids broke up food in different ways. However, the magnitudes of the differences were small and the hominids were in fact broadly similar, suggesting broadly similar diets.

The present research contributes to anthropology by exploring new ways to address the issue of hominid diets. It was the first to apply a mathematical model to the investigation of masticatory differences, the first to calculate symphyseal torque (Hylander ('84) and White ('77) estimated it), and the first to apply a three dimensional model of jaw closure. The computer assisted model has potential value in testing the validity of reconstructions of hominid skulls.

Finally, the potential for future research is considerable.

(1) The computer assisted model can be used to determine the bite force directions that each hominid is designed to produce efficiently, thus revealing more closely the possible range of foods eaten. However, each hominid must first be represented more realistically - with individual muscle maxima and joint reaction force

directions. A technique for finding ratios of maximum muscle tension in hominids needs to be devised. In the present study, the muscle maxima were held constant for all the hominids. Judging by the size and shape of their attachment sites, the maxima were not the same and, for some hominids, the ratios were also different. More accurate joint reaction force directions should be used, since the articular surfaces in the joint probably remodel in response to average muscle activity, in turn a response to the properties of the diet. In the present study, only one joint reaction force direction was used for all of the hominids. The balancing needs of the system would differ for different directions. The relationship between that joint reaction force direction and the directions of the main bite force producing muscles would also be of considerable interest.

In addition, unilateral bite forces with components in the frontal projection should be investigated. Food is usually broken up on one side of the mouth at a time and there is a medial component in the power stroke. In the past, the effect of components of the forces in the sagittal projection has been considered while the effect of those in the frontal projection has not.

A technique for scaling the hominid skulls should also be developed so that the way in which two hominids differ morphologically can be determined. For example, does the direction of the masseter muscle of I2 differ from that of I1 because its zygomatic arch is shorter, because its face is deeper, or both?

(2) The study of symphyseal torque has considerable potential. The relationship between symphyseal morphology and patterns and magnitudes of symphyseal torque needs to be explored.

(3) The crush:shear research can be expanded, taking into account the orientations of the teeth with respect to their paths of closure, so that adaptations for improved crushing or shearing can be revealed. The ultimate value of such a study concerns the information it might provide about the properties of the food eaten. The directions and forces required to break up foods with different properties should first be determined.

(4) Finally, and perhaps most important, the range of variation in the hominids, both extinct and extant, needs to be investigated in order that the significance of the differences between them can be understood. At the same time the sensitivity of the models can be examined by testing the effect of small changes in the attributes of the system.

Table 1 Hominids included in the present study. A.L., Afar Locality; Anth., Anthropology Museum, University of Alberta; Dent., Dentistry Museum, University of Alberta; KNM-ER, Kenya National Museums-East Rudolph; SK, Swartkrans; STS, Sterkfontein Type Site, U.M.P., University Museum, Pennsylvania.

Hominid	Specimen Number	Text
Category 1:		
1. Indian 1	Dent.17.636	I1
2. Indian 2	Dent.19.787	I2
3. Amerindian	Anth.968.11.1	AI
4. Australian Aborigine	Anth.971.1.1	AA
5. Bushman	U.M.P.500	BM
6. Skhul V	U.M.P.605	SV
7. La Chapelle-aux-Saints	U.M.P.490	CS
8. Peking Man	U.M.P.587	PM
Category 2:		
9. Rhodesian Man	U.M.P.471 U.M.P.440	RM
10. Robust Australopithecine	KNM-ER406 KNM-ER729	RA
11. Gracile Australopithecine	STS-5 SK-23	GA
Category 3:		
12. African Erectus	KNM-ER3733	AE
13. Habiline Hominid 1	KNM-ER1813	H1
2		H2
Category 4:		
14. Afar Hominid	A.L.333-1	AH

Table 2 The parts of the masticatory muscles used in the present study.

Muscle	Designated Part	Text
Temporalis	1. Anterior	Ta
	2. Middle	Tm
	3. Posterior	Tp
Masseter	4. Superficial Anterior	Msa
	5. Superficial Posterior	Msp
	6. Deep Anterior	Mda
	7. Deep Posterior	Mdp
Medial Pterygoid	8. Anterior	Pma
	9. Posterior	Pmp
Lateral Pterygoid	10. Superior	Pls
	11. Middle	Plm
	12. Inferior	Pli

Table 3 Calculation of muscle force maximums. a., physiological cross sections (cm^2) of Weijs and Hillen ('85); b., maximum force (a. x 3.5) in kg; c., proportions of the muscle parts; d., the maximum force of the parts used in the present study (b. x c.) in kg; e., maximums used by Osborn and Baragar ('85), in kg.

Muscle	a.	b.		c.	d.	e.
Temporalis	10.9	38.2	Ta	.43	16.5	27.0
			Tm	.30	11.5	17.0
			Tp	.26	10.0	16.0
Masseter	9.2	32.2	Msa	.35	11.2	14.0
			Msp	.29	9.3	13.0
			Mda	.18	5.8	10.0
			Mdp	.20	6.5	9.0
Medial Pterygoid	6.6	23.1	Pma	.26	6.0	8.0
			Pmp	.74	17.1	18.0
Lateral Pterygoid	3.1	10.9	Pls	.29	3.2	12.0
			Plm	.37	4.0	13.0
			Pli	.34	3.7	14.0

Table 4 Three dimensional coordinates of the left muscle attachments and the bite points for Indian 1 (cm). Primed coordinates are in the mandible.

	x'	y'	z'	x	y	z
Ta	3.4	4.2	-1.4	3.7	4.5	4.3
Tm	2.7	3.7	-1.3	0.4	5.5	4.6
Tp	2.2	4.2	-0.8	-2.0	6.1	3.0
Msa	3.2	3.9	-4.8	5.6	4.9	-0.6
Msp	1.5	4.4	-3.5	3.6	6.0	-0.1
Mda	3.2	3.9	-3.0	4.1	5.8	-0.3
Mdp	2.0	4.1	-1.7	1.8	5.8	-0.6
Pma	2.2	3.6	-4.6	3.2	2.0	-2.4
Pmp	1.1	3.9	-3.4	2.6	1.7	-1.0
Pls	0.2	4.0	0.0	2.0	2.7	0.4
Plm	0.5	4.2	-0.8	2.1	1.9	-0.4
Pli	0.9	4.1	-1.1	2.6	2.1	-1.3
J	0.1	4.4	0.2	-29.8	-15.7	-93.3
I1	8.2	0.0	-2.6	-	-	-
M1	5.8	2.3	-2.9	-	-	-

Table 5 Three dimensional coordinates of the left muscle attachments and the bite points for Indian 2 (cm). Primed coordinates are in the mandible.

	x'	y'	z'	x	y	z
Ta	2.9	4.0	-1.5	3.2	4.8	4.6
Tm	2.0	3.7	-2.2	0.5	5.5	3.1
Tp	2.5	4.4	-0.5	-1.0	6.0	2.7
Msa	2.8	4.1	-5.6	4.5	4.7	-0.6
Msp	0.7	4.8	-4.3	3.1	5.6	-0.1
Mda	2.5	4.0	-2.8	3.5	5.0	-0.2
Mdp	1.5	4.5	-1.8	2.1	5.5	0.7
Pma	1.2	4.0	-5.7	2.5	2.2	-2.0
Pmp	0.3	4.3	-3.8	2.0	1.7	-0.5
Pls	0.0	4.4	0.6	1.3	3.4	1.0
Plm	0.0	4.6	0.3	1.5	1.8	0.2
Pli	-0.1	4.6	-0.1	2.0	2.1	-1.0
J	-0.1	4.8	0.7	-29.8	-15.3	-93.3
I1	8.1	0.0	-3.4	-	-	-
M1	5.2	1.9	-3.8	-	-	-

Table 6 Three dimensional coordinates of the left muscle attachments and the bite points for the Amerindian (cm). Primed coordinates are in the mandible.

	x'	y'	z'	x	y	z
Ta	4.1	4.5	-2.4	3.9	4.6	4.7
Tm	2.9	4.1	-2.8	0.9	5.9	2.9
Tp	3.2	4.7	-1.3	-1.1	6.6	3.2
Msa	3.4	5.0	-6.0	6.0	5.2	-0.7
Msp	1.2	5.3	-5.2	4.1	6.4	0.4
Mda	3.4	4.6	-3.7	5.0	5.5	0.1
Mdp	2.0	4.9	-2.6	2.9	6.3	1.0
Pma	2.2	4.8	-6.5	3.5	2.3	-2.9
Pmp	0.9	4.8	-4.7	2.8	2.0	-0.9
Pls	0.2	4.9	0.3	2.3	3.6	1.2
Plm	0.2	4.9	-0.2	2.4	2.2	0.3
Pli	0.2	4.9	-0.6	2.5	2.4	-1.3
J	0.0	5.4	0.5	-29.8	-14.7	-93.3
I1	9.4	0.0	-4.0	-	-	-
M1	7.0	2.5	-4.5	-	-	-

Table 7 Three dimensional coordinates of the left muscle attachments and the bit e points for the Australian Aborigine (cm). Primed coordinates are in the mandible.

	x'	y'	z'	x	y	z
Ta	3.9	4.6	-1.7	4.7	5.3	2.6
Tm	3.1	4.2	-2.7	1.5	5.6	1.3
Tp	3.0	4.8	-0.9	-2.7	6.1	2.0
Msa	3.3	4.7	-5.9	6.1	5.6	-3.0
Msp	1.4	5.4	-5.1	4.4	7.1	-1.9
Mda	3.6	4.8	-3.8	5.3	6.1	-2.2
Mdp	2.0	5.1	-2.5	3.3	7.2	-0.9
Pma	2.4	4.7	-6.0	3.6	3.0	-4.0
Pmp	1.0	4.9	-4.9	3.2	2.7	-2.8
Pls	0.2	4.8	-0.1	2.4	3.9	-0.9
Plm	0.1	4.9	-0.5	2.7	2.7	-1.5
Pli	0.2	5.0	-1.0	2.8	3.0	-2.9
J	0.0	5.2	0.2	-29.8	-14.9	-93.3
I1	10.1	0.0	-3.7	-	-	-
M1	7.2	2.6	-4.1	-	-	-

Table 8 Three dimensional coordinates of the left muscle attachments and the bite points for the Bushman (cm). Primed coordinates are in the mandible.

	x'	y'	z'	x	y	z
Ta	3.6	4.3	-1.5	3.5	4.9	3.3
Tm	2.6	3.8	-1.8	0.7	6.0	3.7
Tp	2.8	4.5	-0.2	-1.6	6.8	2.5
Msa	3.2	4.1	-4.7	5.6	5.2	-1.3
Msp	1.3	4.2	-3.9	3.8	6.1	-1.0
Mda	3.4	4.1	-2.6	4.7	5.3	-0.7
Mdp	1.7	4.5	-2.0	2.2	5.8	-0.3
Pma	2.0	3.9	-4.6	3.3	2.4	-1.9
Pmp	1.1	4.1	-3.2	2.6	2.1	-0.6
Pls	0.4	4.4	0.2	1.8	3.5	0.2
Plm	0.5	4.4	-0.3	2.3	2.6	-0.3
Pli	0.8	4.5	-0.7	3.0	2.5	-1.3
J	0.2	4.6	0.3	-29.8	-15.5	-93.3
I1	8.7	0.0	-2.5	-	-	-
M1	6.0	2.4	-2.7	-	-	-

Table 9 Three dimensional coordinates of the left muscle attachments and the bite points for the Skhul V hominid (cm). Primed coordinates are in the mandible.

	x'	y'	z'	x	y	z
Ta	3.7	4.7	-1.5	2.8	5.3	5.7
Tm	2.3	4.4	-2.1	0.9	6.0	4.0
Tp	2.6	5.3	-0.4	-0.4	6.5	2.7
Msa	3.0	4.1	-5.8	5.3	6.0	0.6
Msp	0.7	4.9	-5.1	4.0	7.0	1.1
Mda	2.8	4.4	-4.3	4.4	6.3	1.2
Mdp	1.9	4.8	-2.8	2.6	7.0	1.5
Pma	1.8	3.8	-6.0	3.3	3.2	-2.1
Pmp	0.6	4.9	-4.2	2.3	2.3	0.1
Pls	0.2	4.7	0.2	1.7	3.7	1.9
Plm	0.3	5.1	-0.1	2.3	2.7	1.0
Pli	0.4	5.3	-0.6	2.3	3.2	-0.5
J	-0.3	5.1	0.3	-29.8	-15.0	-93.3
I1	9.3	0.0	-3.1	-	-	-
M1	6.6	2.2	-3.4	-	-	-

Table 10 Three dimensional coordinates of the left muscle attachments and the bite points for the La Chapelle-aux-Saints Hominid (cm). Primed coordinates are in the mandible.

	x'	y'	z'	x	y	z
Ta	3.8	5.7	-1.3	2.9	4.9	5.7
Tm	2.7	4.8	-1.6	0.3	6.0	4.8
Tp	1.9	5.5	0.2	-3.0	7.2	4.2
Msa	3.1	5.1	-5.1	5.3	5.7	1.5
Msp	0.7	5.6	-3.5	3.6	6.8	1.6
Mda	3.4	5.4	-3.0	4.1	6.0	1.7
Mdp	1.7	5.9	-1.3	2.0	6.9	1.3
Pma	2.0	4.7	-5.0	3.8	2.5	-1.3
Pmp	0.5	6.1	-3.3	2.1	2.3	0.1
Pls	-0.1	5.5	0.7	1.1	4.3	1.7
Plm	-0.1	5.6	0.6	1.4	2.7	0.8
Pli	0.0	5.7	0.3	2.1	2.8	-0.1
J	-0.6	6.4	0.7	-29.8	-14.7	-93.3
I1	10.4	0.0	-2.6	-	-	-
M1	7.8	2.8	-2.7	-	-	-

Table 11 Three dimensional coordinates of the left muscle attachments and the bite points for Rhodesian Man (cm). Primed coordinates are in the mandible.

	x'	y'	z'	x	y	z
Ta	3.6	6.1	-2.2	3.2	4.6	5.0
Tm	2.4	5.3	-2.4	0.2	5.9	4.2
Tp	2.9	6.5	-0.4	-3.7	6.4	3.2
Msa	2.7	5.9	-6.1	5.5	5.6	0.2
Msp	0.7	6.4	-4.4	3.4	6.5	0.5
Mda	3.1	6.2	-3.8	4.8	5.5	0.9
Mdp	1.6	6.6	-2.2	2.8	6.3	1.0
Pma	1.4	5.5	-5.9	4.0	2.2	-2.3
Pmp	0.1	5.7	-4.0	3.1	1.7	0.2
Pls	0.4	5.8	0.3	2.0	3.2	1.3
Plm	0.3	6.0	-0.1	2.5	1.9	0.5
Pli	0.5	6.2	-0.5	2.5	2.0	-0.7
J	-0.2	6.2	0.6	-29.8	-14.7	-93.3
I1	10.3	0.0	-3.6	-	-	-
M1	7.7	3.0	-3.8	-	-	-

Table 12 Three dimensional coordinates of the left muscle attachments and the bite points for Peking Man (cm). Primed coordinates are in the mandible.

	x'	y'	z'	x	y	z
Ta	3.6	4.5	-1.1	3.6	5.0	4.9
Tm	2.7	3.9	-1.2	1.1	5.9	3.4
Tp	2.3	4.6	0.1	-1.2	6.5	2.3
Msa	3.2	4.6	-4.8	5.2	5.1	-0.1
Msp	1.1	5.0	-4.0	3.2	6.6	0.5
Mda	3.3	4.6	-2.6	4.0	5.9	1.0
Mdp	1.7	5.0	-1.7	1.9	6.7	0.9
Pma	2.5	4.2	-4.8	3.6	2.3	-2.1
Pmp	0.7	4.7	-3.5	3.0	2.4	-0.5
Pls	-0.2	5.2	0.5	1.8	3.7	1.1
Plm	-0.1	4.9	0.0	2.2	2.6	0.2
Pli	0.1	5.1	-0.2	2.3	2.5	-1.2
J	-0.8	5.4	0.5	-29.8	-14.7	-93.3
I1	9.6	0.0	-2.5	-	-	-
M1	6.7	2.8	-2.5	-	-	-

Table 13 Three dimensional coordinates of the left muscle attachments and the bite points for the African Erectus (cm). Primed coordinates are in the mandible.

	x'	y'	z'	x	y	z
Ta	3.5	4.0	-0.7	2.9	4.5	5.3
Tm	1.3	3.6	0.5	-0.3	5.6	5.1
Tp	0.2	4.1	1.6	-3.3	6.1	3.8
Msa	3.8	5.1	-5.0	5.8	5.6	-0.3
Msp	1.8	4.9	-4.0	3.9	6.5	0.5
Mda	3.0	4.4	-2.8	4.3	5.7	0.6
Mdp	1.8	4.5	-1.9	2.4	6.2	0.7
Pma	2.5	4.3	-5.5	3.6	2.4	-2.8
Pmp	0.2	3.9	-4.4	2.5	1.6	-1.4
Pls	-0.4	4.6	0.2	1.6	3.1	0.8
Plm	-0.2	4.4	-0.4	2.1	2.1	-0.6
Pli	0.7	5.0	-0.7	2.7	2.4	-2.1
J	-0.8	5.0	0.5	-29.8	-15.1	-93.3
I1	9.7	0.0	-3.5	-	-	-
M1	6.5	2.5	-3.9	-	-	-

Table 14 Three dimensional coordinates of the left muscle attachments and the bite points for the Habiline Hominid, modeled on Indian 2 (cm). Primed coordinates are in the mandible.

	x'	y'	z'	x	y	z
Ta	3.0	3.3	-3.1	3.3	4.1	3.0
Tm	1.9	2.9	-0.8	0.4	4.7	4.5
Tp	1.3	3.9	1.2	-2.2	5.5	4.4
Msa	3.7	5.1	-6.0	5.4	5.7	-1.0
Msp	1.4	5.9	-4.7	3.8	6.7	-0.5
Mda	3.7	5.1	-3.0	4.7	6.1	-0.4
Mdp	1.2	5.5	-2.3	1.8	6.5	0.2
Pma	1.0	4.4	-6.3	2.3	2.6	-2.6
Pmp	0.4	5.3	-4.6	2.1	2.7	-1.3
Pls	0.4	4.0	-0.2	1.7	3.0	0.2
Plm	0.1	4.9	-0.9	1.6	2.1	-1.0
Pli	-0.6	5.2	-0.9	1.5	2.7	-1.8
J	0.6	5.0	0.3	-29.8	-15.1	-93.3
I1	7.4	0.0	-3.5	-	-	-
M1	4.8	2.4	-4.0	-	-	-

Table 15 Three dimensional coordinates of the left muscle attachments and the bite points for the Robust Australopithecine (cm). Primed coordinates are in the mandible.

	x'	y'	z'	x	y	z
Ta	5.1	6.0	-2.4	4.7	4.4	2.7
Tm	3.2	5.3	-2.3	1.6	4.1	3.8
Tp	2.8	6.1	0.0	-2.1	4.7	3.7
Msa	4.7	5.9	-8.0	8.8	6.0	-1.6
Msp	1.8	6.1	-6.0	6.5	8.6	-0.2
Mda	4.5	6.3	-3.6	7.4	6.9	-0.8
Mdp	2.4	6.8	-2.1	3.9	8.3	0.3
Pma	3.4	4.9	-7.8	3.5	2.9	-5.4
Pmp	1.0	5.7	-5.8	2.1	2.1	-4.1
Pls	-0.2	5.7	-0.1	2.1	3.4	-1.3
Plm	0.3	5.9	-0.3	1.8	2.8	-2.4
Pli	0.1	6.1	-0.4	2.5	3.3	-3.9
J	-0.5	6.2	0.2	-29.8	-13.9	-93.3
I1	12.5	0.0	-4.2	-	-	-
M1	8.8	3.2	-4.7	-	-	-

Table 16 Three dimensional coordinates of the left muscle attachments and the bite points for the Habiline Hominid, modeled on the Gracile Australopithecine (cm). Primed coordinates are in the mandible.

	x'	y'	z'	x	y	z
Ta	3.3	0.3	-3.0	3.3	4.1	3.0
Tm	1.3	1.3	-2.3	0.4	4.7	4.5
Tp	1.0	3.5	-0.2	-2.2	5.5	4.4
Msa	1.8	3.3	-6.8	5.4	5.7	-1.0
Msp	-0.5	4.4	-5.5	3.8	6.7	-0.5
Mda	2.3	4.0	-4.2	4.7	6.1	-0.4
Mdp	0.9	4.7	-2.5	1.8	6.5	0.2
Pma	0.4	2.7	-5.6	2.3	2.6	-2.6
Pmp	0.0	3.7	-4.0	2.1	2.7	-1.3
Pls	-0.8	3.6	0.0	1.7	3.0	0.2
Plm	-0.9	3.6	-0.4	1.6	2.1	-1.0
Pli	-0.9	4.0	-0.3	1.5	2.7	-1.8
J	0.6	5.0	0.3	-29.8	-15.1	-93.3
I1	7.4	0.0	-3.5	-	-	-
M1	4.8	2.4	-4.0	-	-	-

Table 17 Three dimensional coordinates of the left muscle attachments and the bite points for the Gracile Australopithecine (cm). Primed coordinates are in the mandible.

	x'	y'	z'	x	y	z
Ta	4.1	3.5	-2.8	5.2	7.3	3.2
Tm	2.1	3.2	-3.2	2.3	6.6	3.6
Tp	1.8	4.2	-1.1	-0.6	6.2	3.9
Msa	2.6	3.4	-6.9	6.2	5.8	-1.1
Msp	0.6	4.2	-5.2	4.9	6.5	-0.2
Mda	3.2	3.9	-3.7	5.6	6.0	0.1
Mdp	1.7	4.4	-2.0	2.6	6.2	0.7
Pma	1.4	3.1	-6.8	3.3	3.0	-3.8
Pmp	0.2	3.7	-4.9	2.3	2.7	-2.2
Pls	-0.3	4.2	-0.2	2.2	3.6	0.0
Plm	-0.2	4.2	-0.4	2.3	2.7	-1.0
Pli	0.0	4.2	-0.7	2.4	2.9	-2.2
J	-0.5	4.3	0.3	-29.8	-15.8	-93.3
I1	10.5	0.0	-4.4	-	-	-
M1	6.9	2.5	-5.0	-	-	-

Table 18 Three dimensional coordinates of the left muscle attachments and the bite points for the Afar Hominid (cm). Primed coordinates are in the mandible.

	x'	y'	z'	x	y	z
Ta	5.4	4.5	-2.1	5.7	2.9	3.1
Tm	3.9	3.9	-2.1	2.4	4.1	3.6
Tp	4.0	4.3	-0.6	-0.4	5.5	2.7
Msa	3.1	4.7	-7.3	7.4	6.6	-2.3
Msp	0.9	4.7	-5.7	5.1	6.9	-1.3
Mda	3.4	4.3	-4.0	6.3	6.6	-1.3
Mdp	1.9	4.3	-2.7	3.7	6.7	0.0
Pma	2.3	3.2	-7.7	4.0	1.9	-4.3
Pmp	0.9	3.6	-6.1	3.3	1.2	-3.0
Pls	0.3	4.0	-0.1	3.3	2.8	-1.0
Plm	0.4	4.0	-0.6	3.1	1.4	-1.9
Pli	0.6	4.0	-0.9	3.0	2.0	-3.3
J	0.3	5.0	0.0	-29.8	-15.1	-93.3
I1	11.9	0.0	-5.6	-	-	-
M1	7.9	2.7	-5.4	-	-	-

Table 19 Three dimensional components of the unit vectors for the left muscles.
* more than two standard deviations from the mean.

Muscle	I1	I2	AI	AA	BM	SV	CS	RM	PM	AE	H2	RA	H1	GA	AH	AVG	S.D.
x component:																	
Ta	.05	.05	-.03	.18	-.02	-.12	-.13	-.05	.00	-.10	.05	-.07	.00	.15	.06	.00	.09
Tm	-.35	-.26	-.32	-.35	-.31	-.22	-.35	-.32	-.30	-.30	-.26	-.25	-.12	.03*	-.25	-.26	.10
Tp	-.70	-.70	-.66	-.87	-.78	-.67	-.75	-.88	-.77	-.76	-.70	-.78	-.54	-.41*	-.78	-.72	.12
Msa	.49	.32	.44	.68	.56	.33	.32	.41	.39	.39	.32	.54	.50	.50	.63	.45	.11
Msp	.49	.49	.45	.64	.58	.45	.48	.48	.40	.40	.49	.60	.62	.62	.65	.52	.08
Mda	.23	.34	.38	.64	.50	.27	.15	.34	.18	.34	.34	.71	.48	.48	.63	.40	.16
Mdp	-.07	.22	.23	.44	.23	.14	.11	.35	.06	.19	.22	.47	.27	.27	.45	.24	.14
Pma	.35	.30	.28	.42	.39	.36	.39	.47	.32	.32	.30	.03*	.53	.53	.42	.36	.12
Pmp	.42	.38	.37	.59	.42	.32	.30	.46	.52	.52	.38	.27	.59	.59	.52	.44	.10
Pls	.80	.77	.80	.88	.84	.61	.61	.50*	.78	.78	.77	.66	.97	.97	.89	.78	.13
Plm	.57	.47	.63	.73	.71	.60	.46	.47	.71	.71	.47	.37	.84	.84	.68	.62	.14
Pli	.65	.62	.66	.69	.73	.67	.58	.43*	.62	.56	.62	.47	.77	.77	.61	.63	.09
J	-.30	-.30	-.30	-.30	-.30	-.29	-.29	-.29	-.29	-.29	-.30	-.29	-.30	-.29	-.30	-.30	.00
y component:																	
Ta	.05	.13	.01	.16	.12	.08	-.11	-.20	.08	.08	.13	-.30	.54	.53	-.29	.07	.23
Tm	.27	.31	.29	.31	.35	.25	.17	.09	.38	.38	.31	-.19*	.44	.45	.03	.26	.16
Tp	.32	.32	.29	.20	.41	.27	.26	-.01	.42	.44	.32	-.22*	.34	.34	.21	.26	.17
Msa	.20	.11	.03	.22	.26	.27	.09	-.04	.10	.10	.11	.01	.33	.33	.28	.16	.11
Msp	.37	.16	.17	.36	.44	.29	.20	.02*	.31	.31	.16	.32	.33	.33	.34	.27	.11
Mda	.49	.34	.21	.49	.46	.31	.13	-.14*	.33	.34	.34	.15	.42	.42	.50	.32	.17
Mdp	.59	.36	.35	.71	.59	.45	.36	-.09*	.55	.54	.36	.47	.53	.53	.59	.46	.18
Pma	-.55	-.42	-.55	-.59	-.45	-.14	-.47	-.60	-.55	-.55	-.42	-.64	-.03	-.03	-.32	-.42	.20
Pmp	-.61	-.57	-.55	-.59	-.55	-.49	-.71	-.61	-.52	-.52	-.57	-.87*	-.28	-.28	-.52	-.55	.14
Pls	-.58	-.59	-.49	-.36	-.54	-.40	-.61	-.81	-.58	-.58	-.59	-.66	-.23	-.23	-.36	-.51	.16
Plm	-.81	-.88	-.77	-.62	-.71	-.72	-.89	-.87	-.71	-.71	-.88	-.77	-.50	-.50	-.66	-.73	.12
Pli	-.76	-.74	-.72	-.53	-.66	-.74	-.80	-.90	-.73	-.73	-.74	-.55	-.42	-.42	-.51	-.66	.14
J	-.20	-.20	-.20	-.20	-.20	-.20	-.20	-.20	-.20	-.20	-.20	-.20	-.20	-.20	-.20	-.20	.00
z component:																	
Ta	1.00	.99	1.00	.97	.99	.99	.99	.98	1.00	.99	.99	.95	.84*	.83*	.95	.96	.05
Tm	.90	.91	.90	.88	.88	.94	.92	.95	.87	.87	.91	.95	.89	.89	.97	.91	.03
Tp	.64	.64	.69	.44	.48	.69	.61	.48	.48	.48	.64	.59	.77	.85*	.59	.60	.11
Msa	.85	.94	.90	.70	.79	.91	.95	.91	.92	.92	.94	.84	.80	.80	.73	.86	.08
Msp	.79	.86	.87	.68	.68	.85	.85	.88	.86	.86	.86	.74	.72	.72	.68	.79	.08
Mda	.84	.88	.90	.60	.73	.91	.98	.93	.93	.88	.88	.69	.77	.77	.59	.82	.12
Mdp	.80	.91	.91	.54*	.77	.88	.93	.93	.84	.82	.91	.75	.80	.80	.67	.82	.10
Pma	.76	.86	.79	.69	.81	.92	.79	.65*	.78	.78	.86	.77	.84	.84	.85	.80	.07
Pmp	.67	.73	.75	.56	.72	.81	.64	.64	.68	.68	.73	.41*	.76	.76	.67	.68	.09
Pls	.18	.24	.34	-.32	.00	.69	.51	.31	.23	.23	.24	-.35	.08	.08	-.27	.15	.28
Plm	.14	-.03	.14	-.28	.00	.33	.06	.13	.06	-.06	-.03	-.52*	-.20	-.20	-.33	-.05	.21
Pli	-.08	-.27	-.20	-.50	-.20	.04	-.11	-.04	-.28	-.39	-.27	-.69	-.48	-.48	-.61	-.30	.21
J	-.93	-.93	-.93	-.93	-.93	-.93	-.94	-.93	-.94	-.94	-.93	-.93	-.93	-.93	-.93	-.93	.00

Table 20 Moment arms of the masticatory muscles of the hominids, calculated about the origin (cm).
* more than two standard deviations from the mean.

	I1	I2	AI	AA	BM	SV	CS	RM	PM	AE	H2	RA	H1	GA	AH	AVG	S.D.
Ta	3.38	3.10	4.02	4.18	3.36	3.75	4.11	3.64	4.40	4.16	2.56	5.38	2.70	5.08	5.21	3.94	.83
Tm	1.88	1.23	1.64	1.80	1.58	2.00	2.28	1.52	2.75	1.98	.95	2.95	.35*	2.70	2.95	1.90	.72
Tp	.67	.87	1.07	.38	.93	1.60	1.19	.61	1.31	1.46	1.14	1.83	.04*	1.47	1.74	1.09	.49
Msa	5.17	4.77	5.92	6.61	5.33	5.17	5.34	5.37	5.76	6.39	4.96	8.80*	4.76	6.43	6.88	5.84	1.03
Msp	3.14	3.18	3.69	4.65	3.58	3.42	3.21	3.20	3.63	4.26	3.18	5.69*	2.95	4.42	4.37	3.77	.73
Mda	3.83	3.68	4.76	5.38	4.28	4.26	4.50	4.60	4.62	4.73	4.08	6.21*	3.84	5.26	5.04	4.60	.65
Mdp	1.73	2.14	2.69	3.26	2.09	2.67	2.51	2.67	2.66	3.07	1.19	3.68	1.17	2.81	2.83	2.48	.68
Pma	3.90	3.35	4.45	5.25	3.75	4.22	4.83	5.10	5.06	5.32	2.57*	4.23	2.99	5.40	5.23	4.38	.88
Pmp	2.76	2.42	3.13	4.38	2.53	2.49	2.70	2.92	3.62	3.78	2.07	4.52	2.17	3.75	4.21	3.16	.79
Pls	.22	.13	.26	.21	.10	.44	.32	.57	.17	.40	.42	.13	.19	.51	.10	.28	.15
Plm	1.07	.39	.73	.62	.60	.64	.17	.81	.56	.85	1.23	.36	1.03	.61	.50	.68	.28
Pli	1.20	.74	.99	.85	.81	.94	.28	1.03	.27	.12	1.58	.16	1.30	.58	.42	.75	.43

Table 21 The component of the unit vector parallel to the bite reaction forces (in the sagittal plane).
* more than two standard deviations from the mean.

	I1	I2	AI	AA	BM	SV	CS	RM	PM	AE	H2	RA	H1	GA	AH	AVG	STD
Bite Reaction Direction: theta=180, phi=0																	
Ta	-1.00	-.99	-1.00	-.97	-.99	-.99	-.99	-.98	-1.00	-.99	-.99	-.95	-.84	-.83	-.95	-.96	.05
Tm	-.90	-.91	-.90	-.88	-.88	-.94	-.92	-.95	-.87	-.87	-.91	-.95	-.89	-.89	-.97	-.91	.03
Tp	-.64	-.64	-.69	-.44	-.48	-.69	-.61	-.48	-.48	-.48	-.64	-.59	-.77	-.85*	-.59	-.60	.11
Msa	-.85	-.94	-.90	-.70*	-.79	-.91	-.95	-.91	-.92	-.92	-.94	-.84	-.80	-.80	-.73	-.86	.08
Msp	-.79	-.86	-.87	-.68	-.68	-.85	-.85	-.88	-.86	-.86	-.86	-.74	-.72	-.72	-.68	-.79	.08
Mda	-.84	-.88	-.90	-.60	-.73	-.91	-.98	-.93	-.93	-.88	-.88	-.69	-.77	-.77	-.59	-.82	.12
Mdp	-.80	-.91	-.91	-.54*	-.77	-.88	-.93	-.93	-.84	-.82	-.91	-.75	-.80	-.80	-.67	-.82	.10
Pma	-.76	-.86	-.79	-.69	-.81	-.92	-.79	-.65*	-.78	-.78	-.86	-.77	-.84	-.84	-.85	-.80	.07
Pmp	-.67	-.73	-.75	-.56	-.72	-.81	-.64	-.64	-.68	-.68	-.73	-.41*	-.76	-.76	-.67	-.68	.09
Pls	-.18	-.24	-.34	.32	.00	-.69	-.51	-.31	-.23	-.23	-.24	.35	-.08	-.08	.27	-.15	.28
Plm	-.14	.03	-.14	.28	.00	-.33	-.06	-.13	-.06	.06	.03	.52*	.20	.20	.33	.05	.21
Pli	.08	.27	.20	.50	.20	-.04	.11	.04	.28	.39	.27	.69	.48	.48	.61	.30	.21
J	.93	.93	.93	.93	.93	.93	.94	.93	.94	.94	.93	.93	.93	.93	.93	.93	.00
Bite Reaction Direction: theta=160, phi=180																	
Ta	-.96	-.95	-.93	-.97	-.92	-.89	-.88	-.90	-.94	-.89	-.95	-.87	-.79*	-.83	-.91	-.91	.05
Tm	-.72	-.76	-.73	-.71	-.72	-.81	-.74	-.78	-.71	-.71	-.76	-.81	-.79	-.85	-.82	-.76	.04
Tp	-.36	-.36	-.42	-.11	-.18	-.42	-.31	-.15	-.19	-.19	-.36	-.29	-.54	-.66*	-.29	-.32	.15
Msa	-.97	-.99	-1.00	-.89	-.93	-.97	-1.00	-1.00	-1.00	-1.00	-.99	-.97	-.92	-.92	-.90	-.96	.04
Msp	-.91	-.98	-.97	-.86	-.84	-.95	-.96	[illegible]	-.94	-.94	-.98	-.90	-.89	-.89	-.86	-.92	.05
Mda	-.87	-.94	-.98	-.78	-.86	-.95	-.97	[illegible]	-.93	-.94	-.94	-.89	-.89	-.89	-.77*	-.91	.06
Mdp	-.73	-.93	-.93	-.66*	-.80	-.87	-.91	-.99	-.81	-.83	-.93	-.87	-.84	-.84	-.78	-.85	.08
Pma	-.83	-.91	-.84	-.79	-.90	-.99	-.88	-.77	-.84	-.84	-.91	-.73	-.97	-.97	-.94	-.87	.07
Pmp	-.77	-.82	-.83	-.73	-.82	-.87	-.70	-.76	-.82	-.82	-.82	-.48*	-.92	-.92	-.81	-.79	.10
Pls	-.44	-.49	-.59	.00	-.29	-.86	-.69	-.47	-.48	-.48	-.49	.10*	-.41	-.41	-.05	-.40	.25
Plm	.33	-.13	-.35	.01	-.24	-.52	-.22	-.23	-.30	-.19	-.13	.36*	-.10	-.10	.08	-.12	.23
Pli	-.15	.04	-.04	.23	-.06	-.27	-.10	-.11	.05	.17	.04	.84*	.19	.60	.75	.15	[illegible]
J	.98	.98	.98	.98	.98	.97	.98	.97	.98	.98	.98	.97	.98	.97	.98	.98	.00

Table 22 The component of the unit vector causing the condyle to slide up (+) or down (-) the eminence.
* more than two standard deviations from the mean.

	I1	I2	AI	AA	BM	SV	CS	RM	PM	AE	M2	RA	H1	GA	AH	AVG	STD
Ta	.26	.26	.34	.13	.33	.41	.41	.35	.29	.39	.26	.37	.31	.13	.25	.30	.08
Tm	.63	.56	.61	.64	.61	.51	.61	.59	.59	.59	.56	.53	.43	.27*	.54	.55	.09
Tp	.91	.91	.88	.99	.97	.88	.93	.98	.97	.97	.91	.94	.80	.68*	.94	.91	.08
Msa	-.21	-.01	-.14	-.44	-.30	-.04	-.03	-.12	-.11	-.11	-.01	-.26	-.24	-.25	-.39	-.18	.13
Msp	-.24	-.20	-.16	-.43	-.38	-.18	-.22	-.19	-.14	-.14	-.20	-.37	-.38	-.39	-.43	-.27	.11
Mda	.05	-.05	-.08	-.48	-.28	.02	.14	-.04	.10	-.08	-.05	-.47	-.24	-.25	-.48	-.15	.20
Mdp	.39	.08	.07	-.36	.03	.15	.18	-.05	.22	.07	.08	-.25	-.01	-.02	-.27	.02	.19
Pma	-.12	-.02	-.03	-.23	-.13	-.07	-.16	-.31	-.10	-.10	-.02	.26*	-.24	-.25	-.14	-.11	.13
Pmp	-.24	-.16	-.14	-.48	-.21	-.07	-.14	-.31	-.35	-.35	-.16	-.27	-.34	-.35	-.34	-.26	.11
Pls	-.86	-.81	-.75	-1.00	-.95	-.40*	-.55	-.65	-.84	-.84	-.81	-.98	-.92	-.92	-1.00	-.82	.17
Plm	-.85	-.97	-.86	-1.00	-.95	-.69*	-.91	-.84	-.93	-.98	-.97	-.80	-1.00	-.99	-.99	-.92	.09
Pli	-.98	-.99	-1.00	-.95	-1.00	-.93	-1.00	-.97	-.99	-.95	-.99	-.78*	-.97	-.96	-.89	-.96	.06

Table 23 The component of the unit vector parallel to the joint reaction force.
* more than two standard deviations from the mean.

	I1	I2	AI	AA	BH	SV	CS	RM	PH	AE	H2	RA	H1	GA	AH	AVG	STD
Ta	-.96	-.96	-.94	-.99	-.94	-.91	-.91	-.93	-.96	-.93	-.96	-.93	-.95	-.99	-.97	-.95	.02
Tm	-.77	-.83	-.79	-.77	-.79	-.86	-.79	-.80	-.81	-.81	-.83	-.84	-.90	-.96*	-.84	-.83	.05
Tp	-.41	-.41	-.47	-.15	-.23	-.47	-.38	-.19	-.26	-.27	-.41	-.33	-.60	-.73*	-.33	-.38	.15
Msa	-.98	-1.00	-.99	-.90*	-.95	-1.00	-1.00	-.99	-1.00	-1.00	-1.00	-.96	-.97	-.96	-.92	-.97	.03
Msp	-.97	-.98	-.99	-.90	-.92	-.98	-.98	-.98	-.99	-.99	-.98	-.93	-.92	-.92	-.90	-.96	.03
Mda	-1.00	-1.00	-1.00	-.88	-.96	-1.00	-.99	-1.00	-1.00	-1.00	-1.00	-.88	-.97	-.96	-.88	-.97	.05
Mdp	-.92*	-1.00	-1.00	-.93	-1.00	-.99	-.99	-.99	-.98	-1.00	-1.00	-.96	-1.00	-1.00	-.96	-.[illegible]8	.03
Pma	-.99	-1.00	-1.00	-.97	-.99	-.99	-.99	-.95	-1.00	-1.00	-1.00	-.96	-.97	-.96	-.99	-.98	.02
Pmp	-.97	-.99	-.99	-.88*	-.98	-.99	-.99	-.95	-.94	-.94	-.99	-.96	-.94	-.93	-.94	-.96	.03
Pls	-.51	-.58	-.66	.03	-.31	-.91	-.84	-.76	-.55	-.55	-.58	.18*	-.39	-.38	-.02	-.46	.31
Plm	-.53	-.25	-.51	.05	-.31	-.72	-.41	-.54	-.37	-.21	-.25	.60*	-.08	-.07	.14	-.23	.32
Pli	-.19	.10	-.02	.31	-.05	-.36	-.11	-.21	.13	.31	.10	.62	.24	.25	.45	.10	.26

Table 24 Bite force efficiency (BF:MF) of the hominids. Blanks indicate no solution to the problem.
* more than two standard deviations from the mean.

	I1	I2	AI	AA	BH	SV	CS	RM	PM	AE	H2	RA	H1	GA	AH	AVG	STD
Bite Force:																	
M1; theta-180, phi-0:																	
10	.60	.69	.65	.53	.59	.63	.57	.53	.63	.66	.86*	.65	.62	.54	.67	.63	.08
40	.62	.66	.63	.54	.62	.61	.54	.52	.62	.67	.83*	.65	.62	.53	.63	.62	.07
50	.61	.63	.60	.52	.59	.59	.49	.47	.59	.63	.78*	.61	.60	.51	.62	.59	.07
70	.55	.56	.52		.53	.49		.39	.53	.56	.72*	.54			.57	.54	.07
M1; theta-160, phi-180:																	
10	.68	.71	.66	.57	.65	.63	.58	.56	.68	.71	.89*	.71	.66	.57	.63	.66	.08
40	.61	.56	.55	.55	.63	.52	.42*	.47	.56	.60	.72*	.64	.61	.55	.62	.57	.07
50	.58	.52	.51	.52	.60	.45	.37*	.43	.54	.56	.66	.60	.56	.52	.57	.53	.07
70	.49	.41	.41	.47	.49				.49	.51	.54		.44	.45	.50	.47	.04
LM1; theta-180, phi-0:																	
10	.62	.68	.65	.52	.62	.63	.57	.53	.63	.67	.78*	.65	.58	.50	.65	.62	.07
40	.60	.64	.60	.51	.58	.59	.52	.51	.57	.61	.73*	.65	.47		.62	.59	.07
50	.58	.61	.58	.48	.55	.56	.47	.47	.54	.56	.70*	.60			.60	.56	.06
70		.54				.50										.52	.02
I1; theta-180, phi-0:																	
10	.45	.49	.50	.40	.43	.47	.44	.41	.48	.49	.60*	.49	.42	.38	.45	.46	.05
40	.43	.40	.46	.38	.40	.42	.37	.35	.43	.44	.49	.43	.36	.36	.40	.41	.04
50	.40	.36	.41		.36	.36	.30	.31	.39	.40	.45	.40			.37	.38	.04
70																	
I1; theta-160, phi-180:																	
10	.51	.52	.52	.43	.46	.49	.46	.44	.51	.53	.63*	.54	.46	.41	.44	.49	.05
40	.43	.36	.41	.39	.41	.34	.29*	.34	.40	.41	.43	.44	.36	.37	.38	.38	.04
50	.38	.29	.38	.36	.35				.38	.39	.38	.36	.30	.34	.35	.36	.03
70																	

Table 25 Maximum bite force in the hominids (kg). V., vertical bite; A. anterior bite. * more than two standard deviations from the mean.

Hominid	Bite Direction:				
	M1 V.	M1 A.	I1 V.	I1 A.	LM1 V.
I1	85	75	60	55	65
I2	90	70	55	50	70
AI	85	70	65	55	65
AA	60	80	45	60	50
BM	75	75	60	55	60
SV	80	60	55	45	75
CS	65	55 *	50	40 *	65
RM	70	60	50	45	60
PM	85	75	60	55	60
AE	90	75	60	55	60
H2	100	75	65	55	65
RA	75	65	60	55	65
H1	65	70	45	50	40
GA	50	75	40*	50	25 *
AH	70	80	50	55	50
AVG	76	71	55	52	58
STD	13	7	7	5	12

Table 26 Joint reaction force in the hominids (kg). Blanks indicate no solution to the problem.
* more than two standard deviations from the mean.

	I1	12	AI	AA	BM	SV	ÇS	RM	PM	AE	H2	RA	H1	GA	AH	AVG	S.D.
Bilateral Vertical Bite on M1:																	
25	4.4	3.9	6.6	2.7	2.5	6.7	9.4	9.4	7.2	3.4	0.0	2.1	3.8	7.3	5.2	5.0	2.6
50	13.5	12.0	13.4	12.1	9.8	15.6	23.5*	21.6	13.7	10.9	3.1	9.3	9.5	17.5	7.9	12.9	5.0
Bilateral Anterior Bite on M1:																	
25	5.1	6.8	7.0	4.9	4.4	8.2	10.7	10.4	6.3	5.3	1.7	3.9	4.0	6.8	5.6	6.1	2.3
50	15.1	19.0	19.4	13.5	13.1	24.2	30.8*	29.3	17.4	16.6	11.8	12.6	13.6	16.9	14.3	17.8	5.7
Bilateral Vertical Bite on I1:																	
25	12.5	14.9	12.2	11.4	12.2	14.6	16.5	17.1	13.9	12.5	7.6*	10.2	12.6	15.4	12.3	13.1	2.4
50	31.9	38.7	30.9		31.1	39.4	47.7	47.7	34.3	29.6	26.3	29.5			30.7	34.8	6.8
Bilateral Anterior Bite on I1:																	
25	12.2	17.0	12.9	12.7	12.4	16.3	18.9*	17.2	14.0	13.0	10.5	10.5	12.4	14.3	13.7	13.9	2.4
50	33.8	47.5*	35.8	30.9	33.8				35.0	33.8	36.3	32.8	45.5	39.9	36.6	36.8	4.8
Unilateral Vertical Bite on LM1:																	
Working Side:																	
25	10.0	2.1	8.8	0.0	1.9	6.9	8.8	6.3	8.3	5.6	.7	0.0	0.0	8.6	0.0	4.5	3.8
50	5.9	4.7	9.0	0.0	0.0	11.4	18.4	19.8*	11.0	7.6	7.4	2.5			3.0	7.7	6.0
Balancing Side:																	
25	.9	6.2	4.0	7.0	6.8	6.2	10.0	12.5	3.9	3.1	1.4	6.5	11.8	16.8*	8.9	7.1	4.2
50	21.3	20.9	20.0	27.7	22.7	22.7	31.1	25.1	19.3	17.8	4.9*	18.5			16.1	20.6	6.0
Ratio of Working Side:Balancing Side:																	
25	11.1*	.3	2.2	.0	.3	1.1	.9	.5	2.1	1.8	.5	.0	.0	.5	.0	1.4	2.7
50	.3	.2	.5	.0	.0	.5	.6	.8	.6	.4	1.5*	.1			.2	.4	.4

Table 27 Three dimensional components of torque per unit tension for the right muscles of mastication and the chosen bite forces
* more than two standard deviations from the mean.

	I1	I2	AI	AA	BM	SV	CS	RM	PM	AE	H2	RA	H1	GA	AH	AVG	STD
x component:																	
Ta	-4.04	-3.45	-4.46	-3.82	-3.90	-4.37	-6.01	-6.66	-4.23	-3.58	-2.96	-6.84	1.10*	-1.00	-5.87	-4.01	1.99
Tm	-2.44	-2.38	-2.76	-2.77	-2.40	-3.39	-3.91	-4.75	-3.14	-.85	-1.18	-5.78*	.25	-1.41	-3.62	-2.64	1.49
Tp	-1.47	-1.25	-1.88	-1.15	-.40	-2.39	-2.11	-3.17	-.28	1.16	-.35	-4.96*	-.89	-1.77	-1.07	-1.47	1.37
Msa	-3.36	-3.88	-4.50	-3.33	-3.29	-3.92	-4.89	-5.35	-4.26	-4.64	-4.85	-4.97	-3.07	-2.89	-3.35	-4.04	.77
Msp	-3.07	-3.95	-4.48	-3.46	-2.59	-4.17	-4.54	-5.61*	-4.15	-3.75	-4.95	-4.45	-3.17	-2.63	-2.55	-3.83	.88
Mda	-2.49	-2.64	-3.66	-1.95	-2.12	-3.76	-5.08	-6.02*	-3.65	-2.95	-3.64	-3.96	-2.53	-1.87	-.74	-3.14	1.29
Mdp	-1.57	-2.80	-3.27	-.48	-1.99	-3.19	-4.30	-6.44*	-2.66	-1.75	-3.85	-3.17	-2.17	-1.19	.01	-2.59	1.55
Pma	-2.74	-3.31	-3.52	-3.07	-3.11	-3.37	-3.53	-3.40	-3.11	-3.35	-3.45	-2.75	-2.27*	-2.59	-2.69	-3.08	.38
Pmp	-3.35	-4.05	-4.32	-3.22	-3.67	-4.41	-4.83	-4.62	-3.72	-3.22	-4.38	-2.69	-3.23	-3.23	-3.19	-3.74	.63
Pla	-3.39	-4.60	-4.75	-.48	-2.54	-5.36	-6.04	-6.58	-4.10	-4.38	-4.09	-2.03	-1.55	-1.76	-1.62	-3.55	1.75
Plm	-3.67	-4.88	-5.15	-1.85	-2.98	-5.28	-4.96	-5.57	-3.49	-3.36	-3.90	-1.48	-1.83	-2.16	-3.30	-3.59	1.32
Pli	-2.33	-2.68	-2.91	.01	-1.61	-3.54	-3.29	-4.34	-1.71	-1.55	-2.00	1.02	-.26	-.38	-.98	-1.77	1.42
J	3.13	3.24	3.72	3.66	3.32	3.66	4.96*	4.53*	4.08	3.50	3.49	4.49	3.49	2.66	3.13	3.67	.59
M1.V	2.30	1.90*	2.50	2.60	2.40	2.20	2.80	3.00	2.80	2.50	2.40	3.20*	2.40	2.50	2.70	2.55	.31
M1.A	2.16	1.79*	2.35	2.44	2.26	2.07	2.63	2.82	2.63	2.35	2.26	3.01*	2.26	2.35	2.54	2.39	.29
I1.V	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.00	.00
I1.A.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.00	.00
y component:																	
Ta	4.56	4.75	4.89	5.76	4.49	4.72	5.51	5.61	5.50	5.06	3.88	5.48	2.94*	5.35	5.46	5.00	.82
Tm	3.44	4.17	4.56	4.23	4.09	5.54	5.48	5.72	4.58	4.99	3.24	7.57*	4.51	7.04	5.32	4.97	1.16
Tp	.92	-.23	.97	-1.49	-.76	1.20	1.22	-1.41	-.28	-1.12	-1.17	.71	1.60	4.71*	-1.45	.23	1.61
Msa	3.81	4.35	5.13	3.92	3.84	5.14	6.21	5.98	5.31	5.07	2.75*	5.33	3.35	5.59	5.81	4.77	1.00
Msp	5.52	6.39	7.23	5.62	5.04	6.97	8.26	8.32	7.08	6.88	5.04	7.82	5.26	7.44	7.97	6.72	1.13
Mda	4.23	5.28	6.00	4.52	4.45	5.77	6.51	6.56	5.74	6.29	3.58	7.16	4.09	6.46	6.63	5.55	1.08
Mdp	4.44	6.25	7.24	5.24	5.58	6.48	7.90	8.54	6.38	6.67	5.80	9.28	5.53	7.75	8.17	6.75	1.32
Pma	4.26	5.33	5.31	4.50	4.98	6.21	6.01	5.12	5.05	5.15	4.75	6.73	5.32	6.93	7.18	5.52	.86
Pmp	4.99	5.86	6.63	5.01	5.66	7.01	6.34	6.75	6.23	6.62	5.01	4.70	6.05	8.26*	7.41	6.17	.97
Pla	5.05	6.42	8.07	2.08	3.95	9.24	8.28	5.77	6.04	6.63	5.62	-.31*	5.94	6.83	3.84	5.56	2.36
Plm	3.19	2.45	4.90	1.28	2.98	5.84	2.99	3.78	3.75	3.06	1.96	-4.00*	2.74	3.02	1.33	2.62	2.11
Pli	1.72	1.23	1.78	-1.21	1.29	3.36	1.76	1.83	.15	-.59	.85	-5.62*	.31	-.36	-2.14	.29	2.08
J	-8.60	-8.90	-10.41	-10.23	-8.88	-10.12	-11.31	-10.82	-10.76	-11.05	-7.51	-13.67*	-7.51	-11.62	-12.05	-10.23	1.65
M1.V	-2.00	-2.30	-2.10	-1.90	-2.20	-2.30	-2.00	-1.80	-2.40	-2.60	-2.00	-3.40*	-2.00	-3.00	-2.90	-2.33	.44
M1.A	-2.46	-2.71	-2.48	-2.33	-2.68	-2.74	-2.53	-2.30	-2.94	-2.99	-2.39	-3.71*	-2.39	-3.30	-3.47	-2.76	.42
I1.V	.40	.60	.30	1.00	.50	.40	.60	.80	.50	.60	.60	.30	.60	.60	1.10*	.59	.22
I1.A.	-.30	-.12	-.40	.26	-.21	-.30	-.12	.07	-.21	-.12	-.12	-.40	-.12	-.12	.35*	-.12	.21
z component:																	
Ta	.43	.80	-.09	1.66	.47	-.15	-1.40	-1.49	.44	.05	.66	-2.55	1.89	3.60*	-1.30	.20	1.48
Tm	.08	.74	.49	.39	.78	.68	-.47	-1.06	1.26	1.88	.76	-3.04*	2.26	3.61*	-.77	.51	1.49
Tp	-1.15	-1.48	-1.39	-2.96	-1.30	-1.85	-2.07	-5.79	-.69	.80	-.97	-6.83*	.08	1.03	-1.93	-1.77	2.06
Msa	2.83	1.83	2.37	4.47	3.60	2.95	2.24	2.15	2.38	2.52	1.97	3.26	3.30	4.11	5.12*	3.01	.94
Msp	4.49	3.44	3.73	6.23	5.47	4.58	4.51	3.25	4.48	4.22	3.76	6.99	5.14	5.67	6.42	4.83	1.09
Mda	3.35	3.06	2.95	5.77	4.26	3.08	1.64	1.21	2.74	3.57	2.79	5.63	3.81	4.69	6.41	3.65	1.43
Mdp	3.14	3.15	3.61	7.29	4.87	3.82	3.57	1.60	4.37	4.80	3.23	7.80	4.40	5.53	7.19	4.56	1.69
Pma	-1.82	-1.45	-2.45	-1.98	-1.27	.37	-1.83	-2.28	-2.29	-2.25	-1.12	-5.49*	1.24	1.39	-1.38	-1.51	1.60
Pmp	-2.45	-2.47	-2.73	-1.89	-2.18	-2.50	-4.77	-3.11	-1.92	-2.60	-1.63	-8.21*	.28	-.53	-3.28	-2.67	1.85
Pla	-1.21	-1.04	-.44	1.03	-.52	-.61	-2.68	-4.47	-1.34	-1.92	-.70	-4.42	1.74	1.73	-.22	-1.01	1.79
Plm	-3.52	-4.44	-3.77	-2.00	-2.34	-3.13	-4.24	-5.18	-3.05	-3.48	-3.59	-6.98*	-.83	-1.52	-4.14	-3.61	1.60
Pli	-2.58	-2.77	-3.17	-1.27	-1.60	-2.74	-4.53	-5.43*	-3.41	-3.33	-2.25	-3.79	-.15	-.92	-2.76	-2.71	1.32
J	-2.86	-2.96	-3.44	-3.38	-2.98	-3.32	-3.94	-3.74	-3.55	-3.43	-2.74	-4.34*	-2.74	-3.30	-3.60	-3.35	.44
M1.V.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.00	.00
M1.A.	.78	-.65	-.85	-.88	-.82	-.75	-.95	-1.02	-.95	-.85	-.82	-1.09	-.82	-.85	-.92	-.76	.42
I1.V.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.00	.00
I1.A.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.00	.00

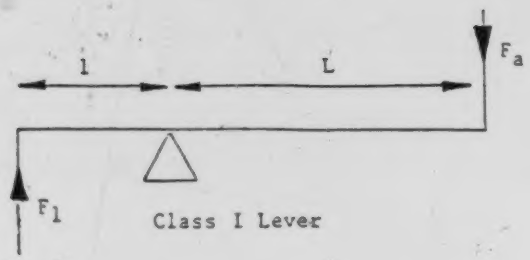
Table 28 Torques at the mandibular symphysis caused by forces on the right side (kg.cm).
* more than two standard deviations from the mean.

	I1	I2	AI	AA	BM	SV	CS	RM	PM	AE	M2	RA	M1	GA	AM	AVG	STD
40kg Bilateral Vertical Bite on I1:																	
x component:	-79.24	-77.68	-98.30	-76.13	-71.38	-95.04	-109.65	-171.87	-78.49	-82.58	-78.56	-169.68	28.03*	-23.26	-105.00	-85.98	46.93
y component:	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.00	.00
z component:	-17.27	-22.57	-47.25	-2.36	5.43	-4.92	-68.31	-119.30*	-32.63	-21.89	8.34	-76.20	48.40	74.44*	-30.04	-20.41	46.16
total:	81.10	80.89	109.07	76.17	71.59	95.87	129.19	209.22*	85.00	85.43	79.00	186.00*	55.93	77.99	109.21	102.12	41.39
40kg Bilateral Anterior Bite on I1:																	
x component:	-82.14	-97.24	-112.11	-79.17	-75.75	-117.66	-151.68	-174.58	-90.08	-93.71	-102.08	-152.56	12.21*	-35.29	-113.38	-97.61	44.59
y component:	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.00	.00
z component:	17.34	-36.42	-29.20	35.26	33.11	-54.86	-205.75*	-131.41	-82.59	-28.33	6.78	-15.61	72.68	97.09	-9.22	-21.41	73.36
total:	83.95	103.84	115.85	86.67	82.67	129.82	255.62*	212.63	122.21	96.94	102.30	153.36	73.70	103.30	113.75	122.44	48.64
40kg Bilateral Vertical Bite on M1:																	
x component:	-34.45	-35.99	-45.38	-27.56	-28.66	-45.02	-55.58	-90.26	-27.21	-34.34	-27.92	-86.25	47.59*	17.39	-59.97	-35.57	33.37
y component:	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.00	.00
z component:	6.25	3.02	-10.54	21.21	18.96	-6.67	-58.24	-73.09	1.01	-2.22	29.23	-58.71	46.45	74.45	-9.21	-1.21	38.14
total:	35.01	36.12	46.59	34.78	34.36	45.51	80.50	116.14*	27.23	34.41	40.42	104.34	66.50	76.45	60.67	55.94	26.58
50kg Bilateral Vertical Bite on M1:																	
x component:	-36.86	-39.96	-52.16	-33.07	-27.28	-55.08	-66.02	-114.08	-29.46	-34.86	-30.14	-108.61	56.43*	24.90	-61.77	-40.53	41.38
y component:	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.00	.00
z component:	13.55	6.90	-17.71	1.78	31.69	1.05	-60.94	-100.81*	-12.82	-9.79	28.03	-67.74	61.17	94.92*	-15.13	-3.06	47.54
total:	39.27	40.55	55.08	33.12	41.88	55.09	89.85	152.24*	32.13	36.21	41.16	128.00	83.22	98.13	63.60	65.96	35.69
80kg Bilateral Anterior Bite on M1:																	
x component:	-41.32	-61.94	-73.14	-35.55	-37.84	-80.75	-109.43	-123.77	-43.59	-50.45	-61.55	-98.29	47.26	10.92	-62.67	-54.81	42.05
y component:	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	.00	.00
z component:	14.18	-7.44	-33.51	26.76	18.15	-37.64	-205.51	-131.08	-74.92	-14.31	17.94	-13.33	57.11	85.30	-13.35	-20.78	70.15
total:	43.69	62.39	80.45	44.50	41.97	89.09	232.83	180.28	86.68	52.44	64.11	99.19	74.13	86.00	64.08	86.79	50.92
50kg Unilateral Vertical Bite on LM1:																	
x component:	-37.61	-44.42	-52.81	-28.39	-26.68	-57.99	-65.57	-115.24*	-27.45	-19.33	-32.73	-107.07	70.21!	17.59!!	-57.93	-51.79!!!	28.81!!!
y component:	-56.33	-32.95	-56.21	-100.17*	-66.32	-39.38	-65.55	-44.82	-66.44	-77.62	-13.69*	-58.14	-16.74	-46.01	-61.64	-56.87	20.52
z component:	-5.53	-11.26	-27.71	33.98	28.85	-19.39	-73.74	-107.84*	-21.96	7.84	2.62	-73.29	65.53	35.21	-11.20	-21.43	39.64
total:	67.96	56.44	81.95	109.52	77.09	73.73	118.46	164.07*	75.17	80.37	35.57	143.18	97.49	60.55	85.33	89.76	33.78

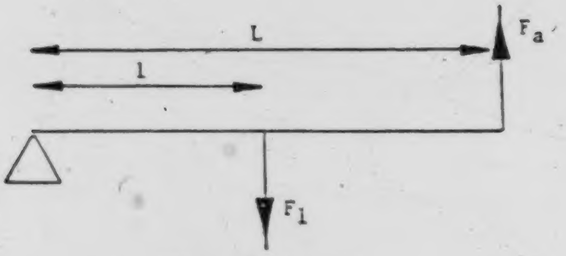
!calculated at 40kg, the maximum for M1
!!calculated at 25kg, the maximum for GA
!!!does not include M1 and GA.

Table 29 Maximum crush:shear in the hominids.* more than two standard deviations from the mean.

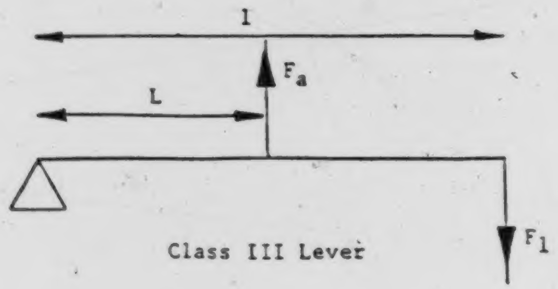
Hominid	h	r	b	C:S for M1:		C:S M1-2cm:	
				K=.25	K=.5	K=.25	K=.5
I1	2.9	5.8	2.1	2.03	1.94	1.42	1.35
I2	3.7	5.1	2.8	1.51	1.45	1.08	1.03
AI	4.4	6.9	3.1	1.66	1.61	1.27	1.23
AA	4.0	7.3	2.5	1.86	1.80	1.41	1.36
BM	2.8	6.0	2.2	2.18	2.08	1.55	1.47
SV	3.4	6.7	2.8	2.05	1.97	1.54	1.48
CS	2.7	7.8	2.7	2.91*	2.78*	2.26*	2.15
RM	3.8	7.7	2.7	2.07	2.00	1.60	1.54
PM	2.5	6.6	2.3	2.65	2.52	1.95	1.85
AE	3.9	6.9	2.5	1.81	1.75	1.36	1.31
H2	4.0	5.4	2.6	1.44	1.39	1.03	.98
RA	4.7	8.8*	3.0	1.92	1.87	1.53	1.49
H1	4.0	5.4	2.6	1.44	1.39	1.03	.98
GA	5.0	6.9	2.8	1.45	1.40	1.09	1.06
AH	5.4	7.9	2.3	1.48	1.44	1.14	1.10
AVG	3.8	6.7	2.6	1.9	1.8	1.4	1.4
STD	.8	1.0	.3	.4	.4	.3	.3



Class I Lever



Class II Lever



Class III Lever

Fig. 1 In Class I levers the fulcrum is located between the applied force, F_a, and the load, F_l. In Class II levers the load is located between the applied force and the fulcrum. In Class III levers the applied force is located between the fulcrum and the load. l, the moment arm of the load; L, the moment arm of the applied force (after Fuller et al., '78).

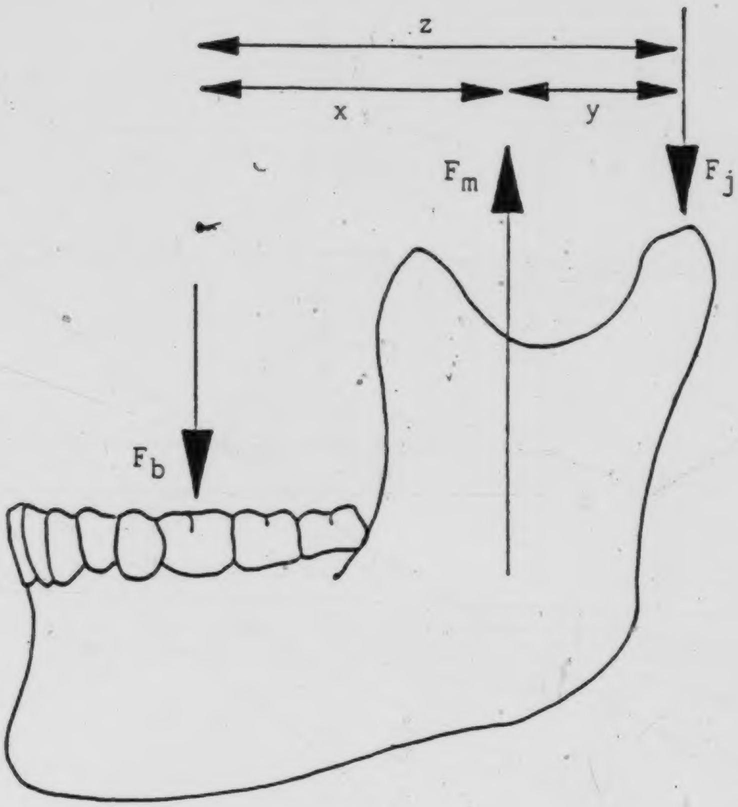


Fig. 2 Sagittal projection of the resultant forces on the human mandible when biting on the first molar. Only the vertical components are shown. F_b, the bite reaction force; F_m, the muscle resultant; F_j, the joint reaction force. F_b and F_m are found by calculating moments about the mandibular condyle: $F_b z + F_m y = 0$. F_j is found by calculating moments about the point of application of F_m: $F_j y + F_b x = 0$, or about the point of application of F_b: $F_j z + F_m x = 0$ (following Hylander, '85).

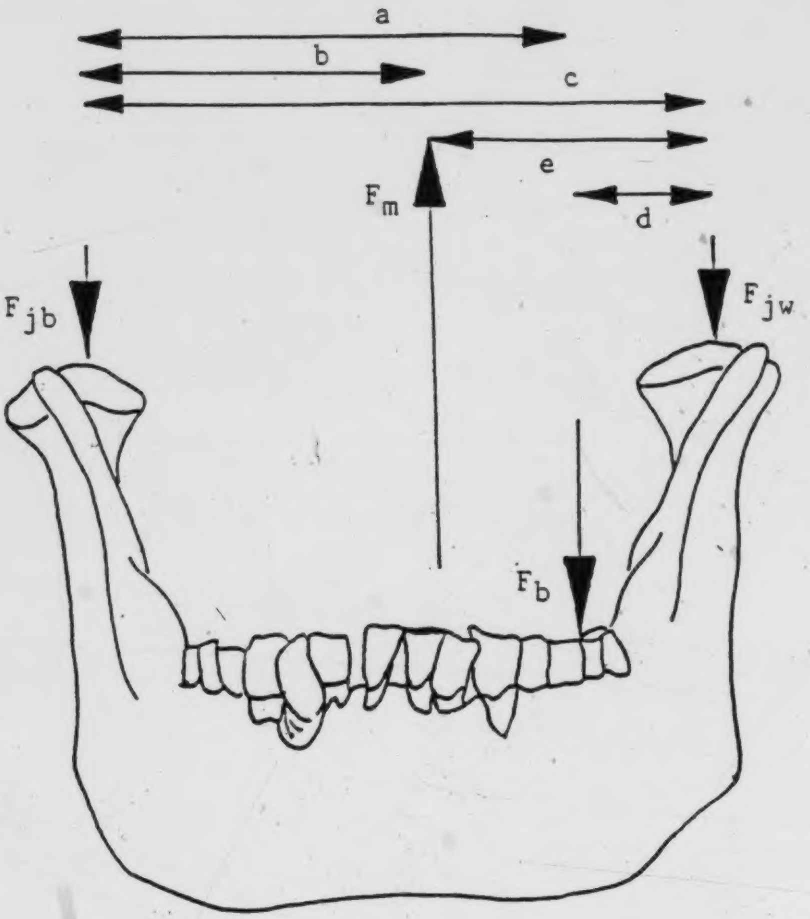


Fig. 3 Frontal projection of the forces on the human mandible when biting on the left first molar. Only the vertical components are shown. F_b, the bite reaction force; F_m, the muscle force; F_{jw}, the w.s. joint reaction force; F_{jb}, the b.s. joint reaction force. F_b, F_m and F_j are found in the sagittal projection. F_{jw} (on the w.s.) is found by calculating moments about the b.s. condyle: $F_b a + F_m b + F_{jw} c = 0$. F_{jb} (on the b.s.) is found by subtracting F_{jw} from F_j or by calculating moments about the w.s. condyle: $F_b d + F_m e + F_{jb} c = 0$ (following Smith, '78).

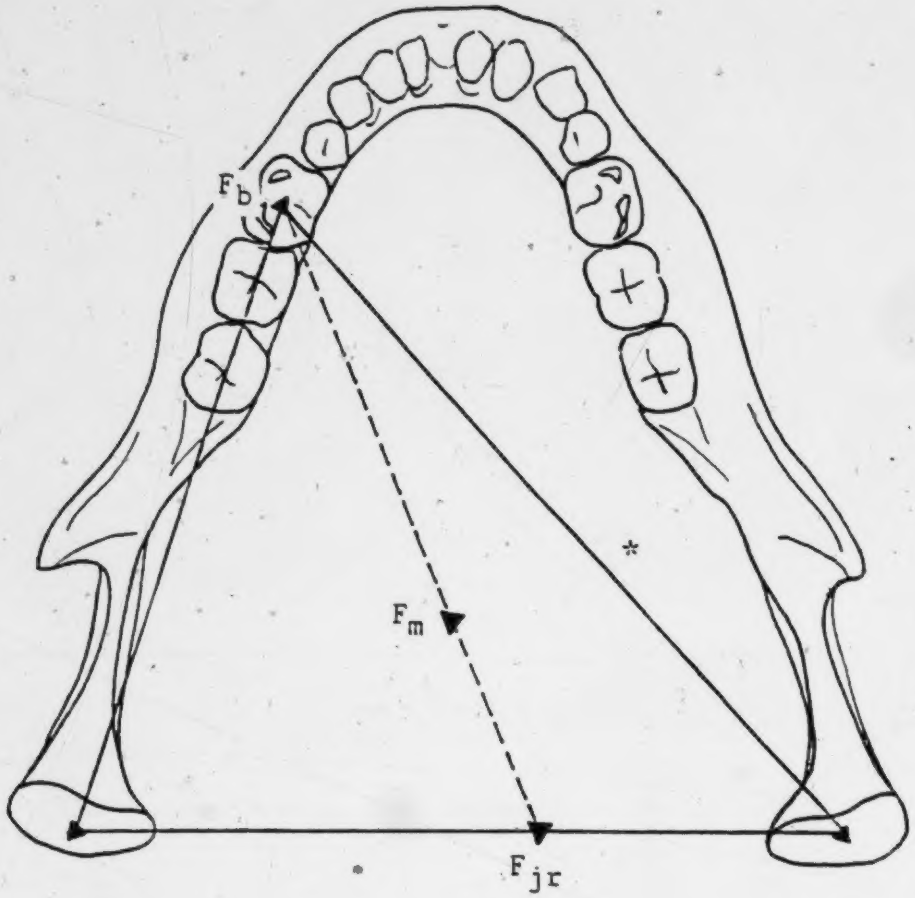
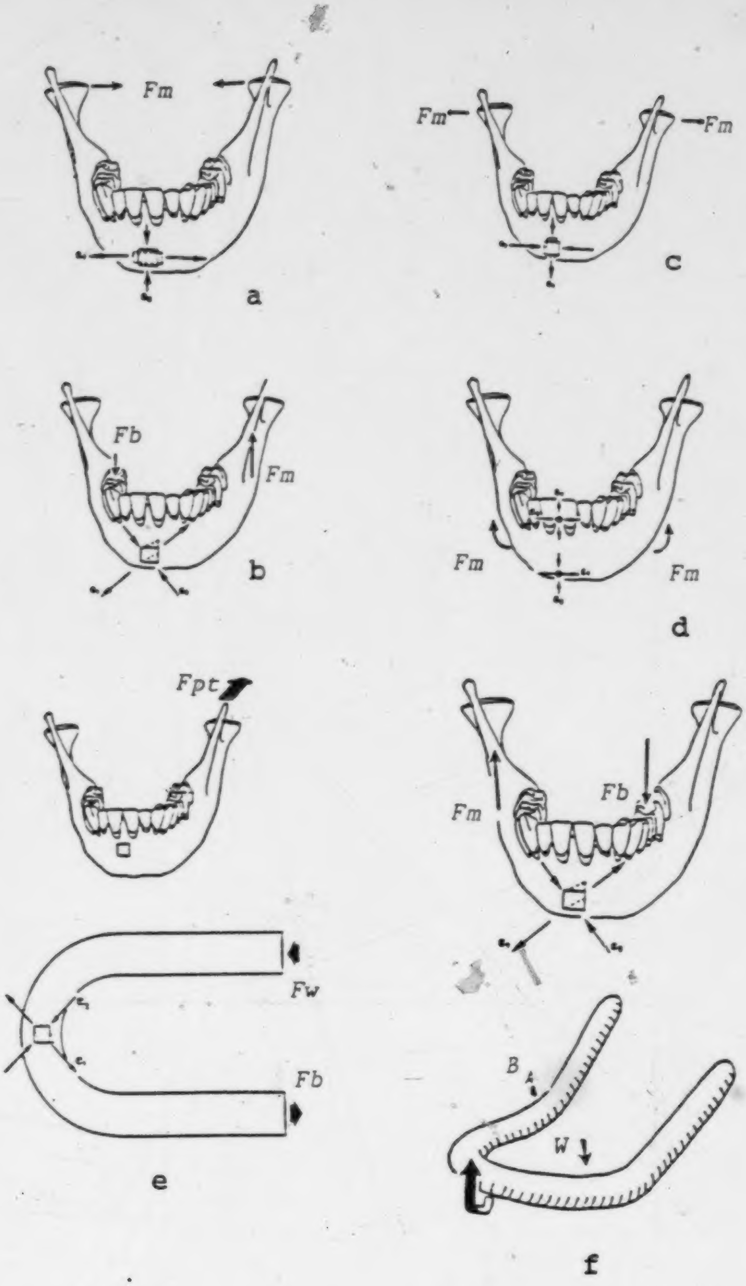


Fig. 4 Occlusal projection of the forces on the human mandible when biting on the left M1. Only the vertical components are shown. F_b, the bite reaction force; F_m, the muscle resultant; F_{jr}, the resultant of the w.s. and b.s. joint reaction forces. For stability the muscle resultant must lie within the triangle of support. If, for example, the resultant is at point *, then the mandible rotates about a line joining the b.s. condyle and the bite point (following Greaves, '78).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f

Fig. 5 Principal bone strains (ε_1 and ε_2), according to Hylander ('84) for six hypothetical patterns of stress. a, medial transverse bending; b, dorsoventral shear; c, lateral transverse bending; d, twisting about the long axes of the mandibular corpora; e, anteroposterior shear; f, twisting about a transverse axis.

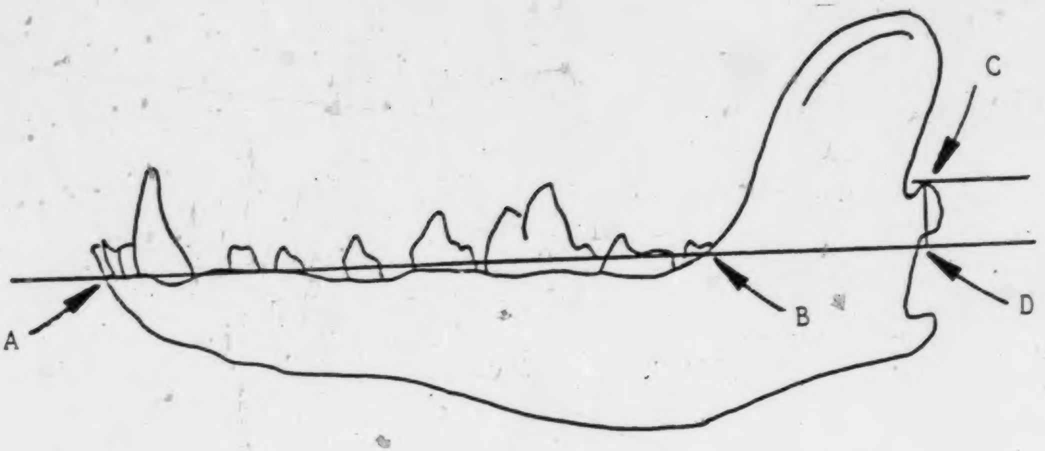

Fig. 6 Hoshi's ('71) condyle height index, 100CD/AD. A, the alveolar border of the central incisor; B, the alveolar border of the last molar; C, the top of the condylar process; D, the foot of the perpendicular.

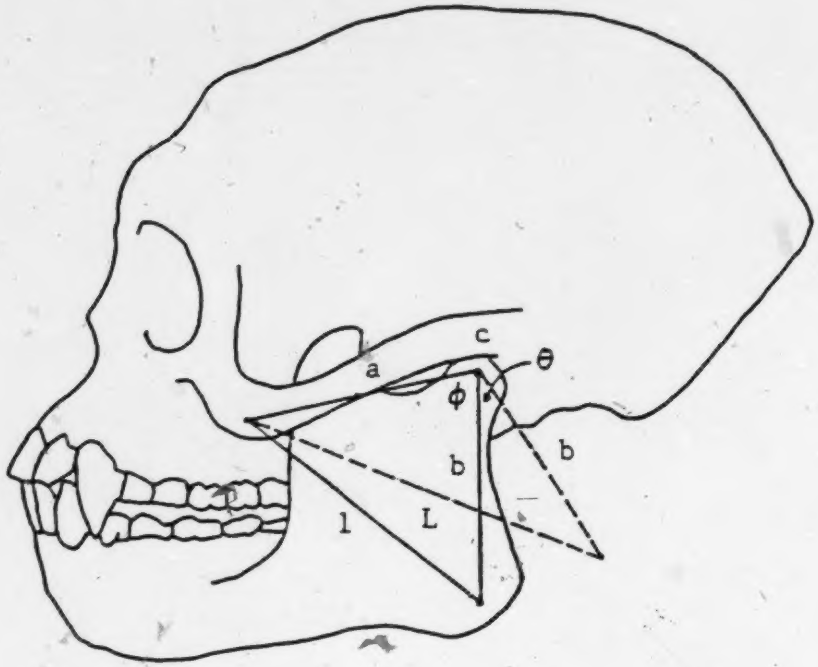

Fig. 7 Following Herring and Herring ('74); a, the distance between the joint (c) and the origin of the superficial masseter; b, the distance between the joint and the insertion of the muscle; l, the length of the muscle in the closed position; L, the length of the stretched muscle; ϕ , the angle between a and b in closed position; θ , the angle through which the mandible is rotated.

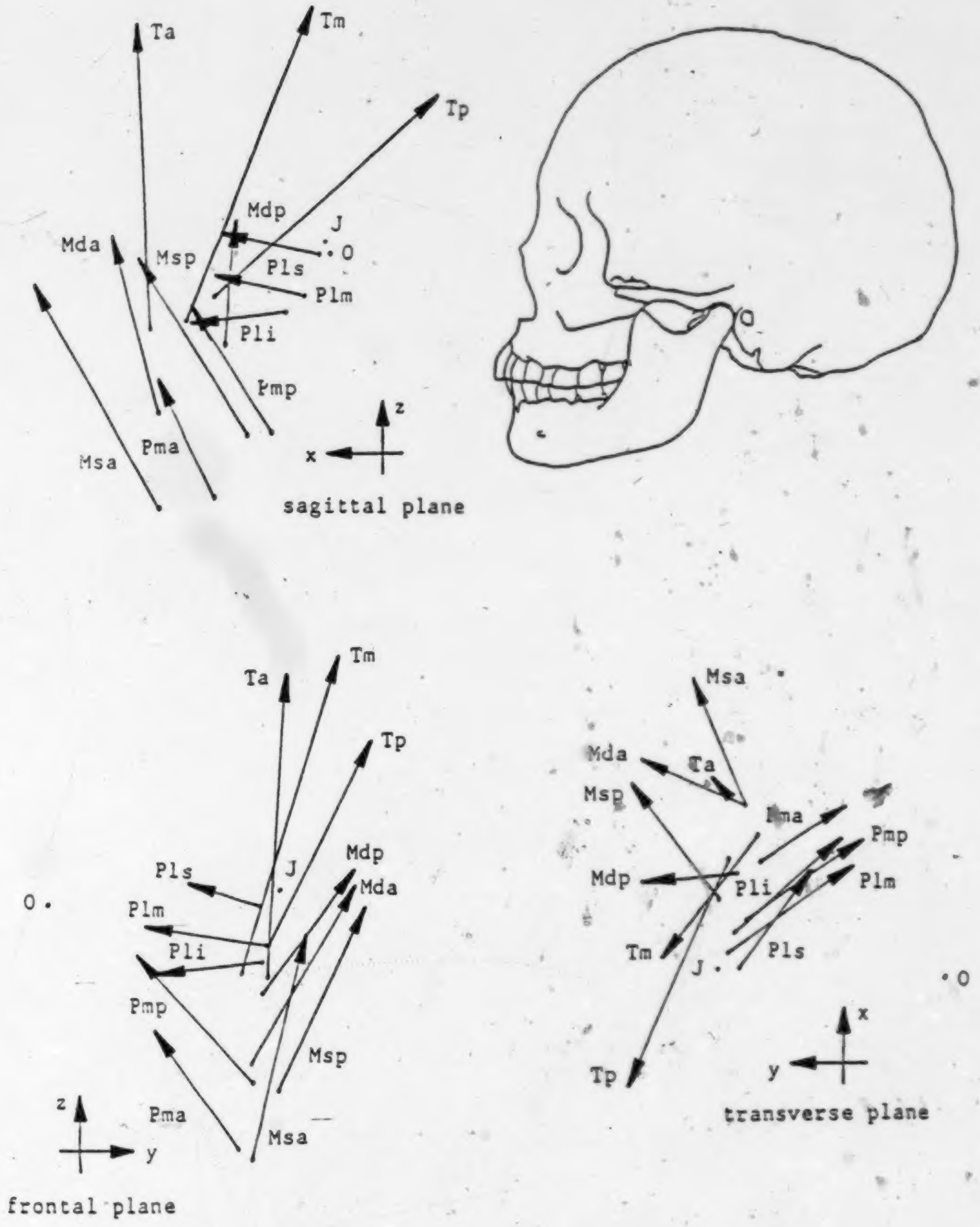
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Fig. 8 The directions of the muscle parts for Indian 1 (I1). Abbreviations are in Table 2. O, the origin of the coordinate system; J, the position of the joint reaction force.

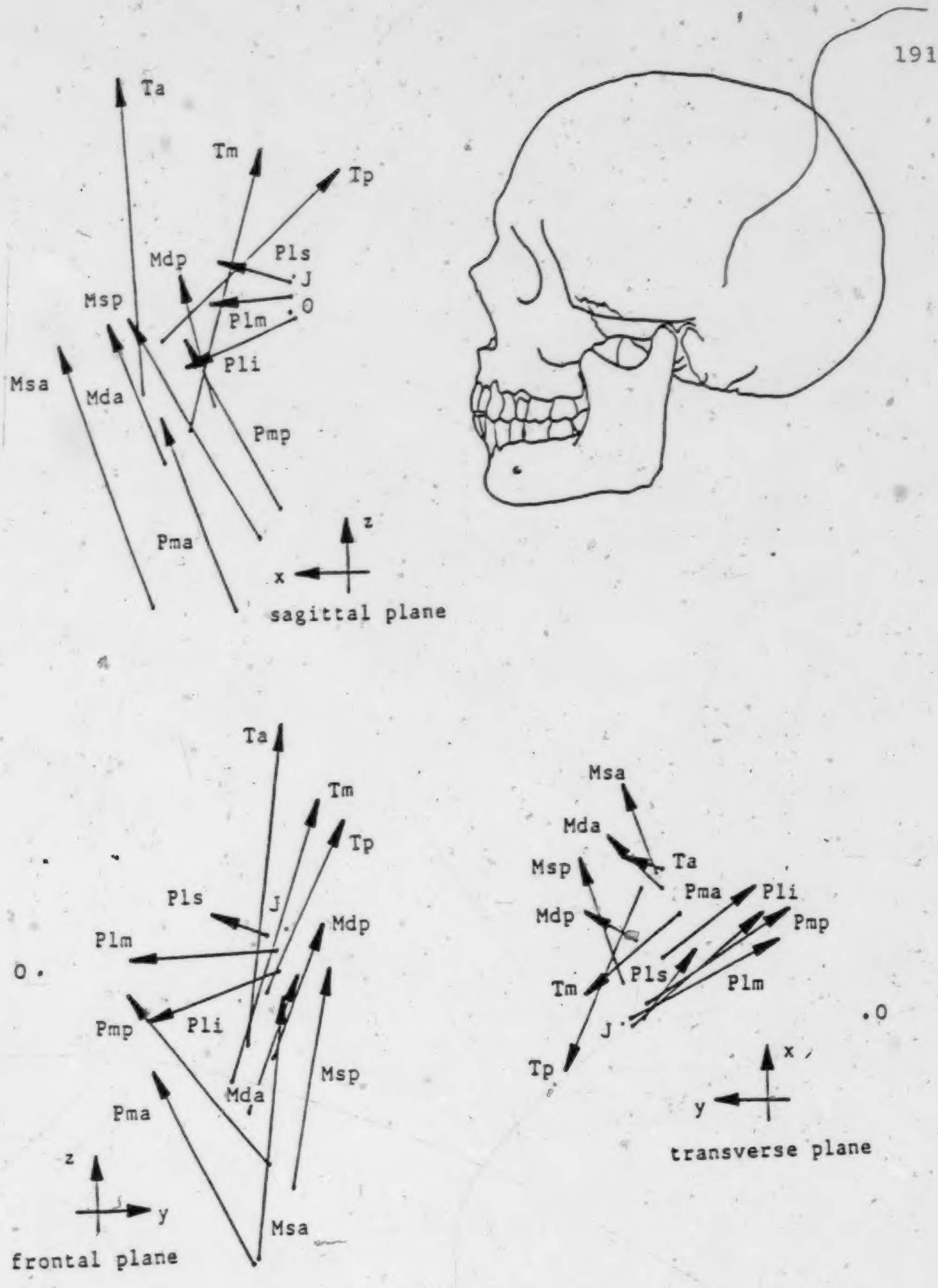
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Fig. 9 The directions of the muscle parts for Indian 2 (I2). Abbreviations are in Table 2. O, the origin of the coordinate system; J, the position of the joint reaction force.

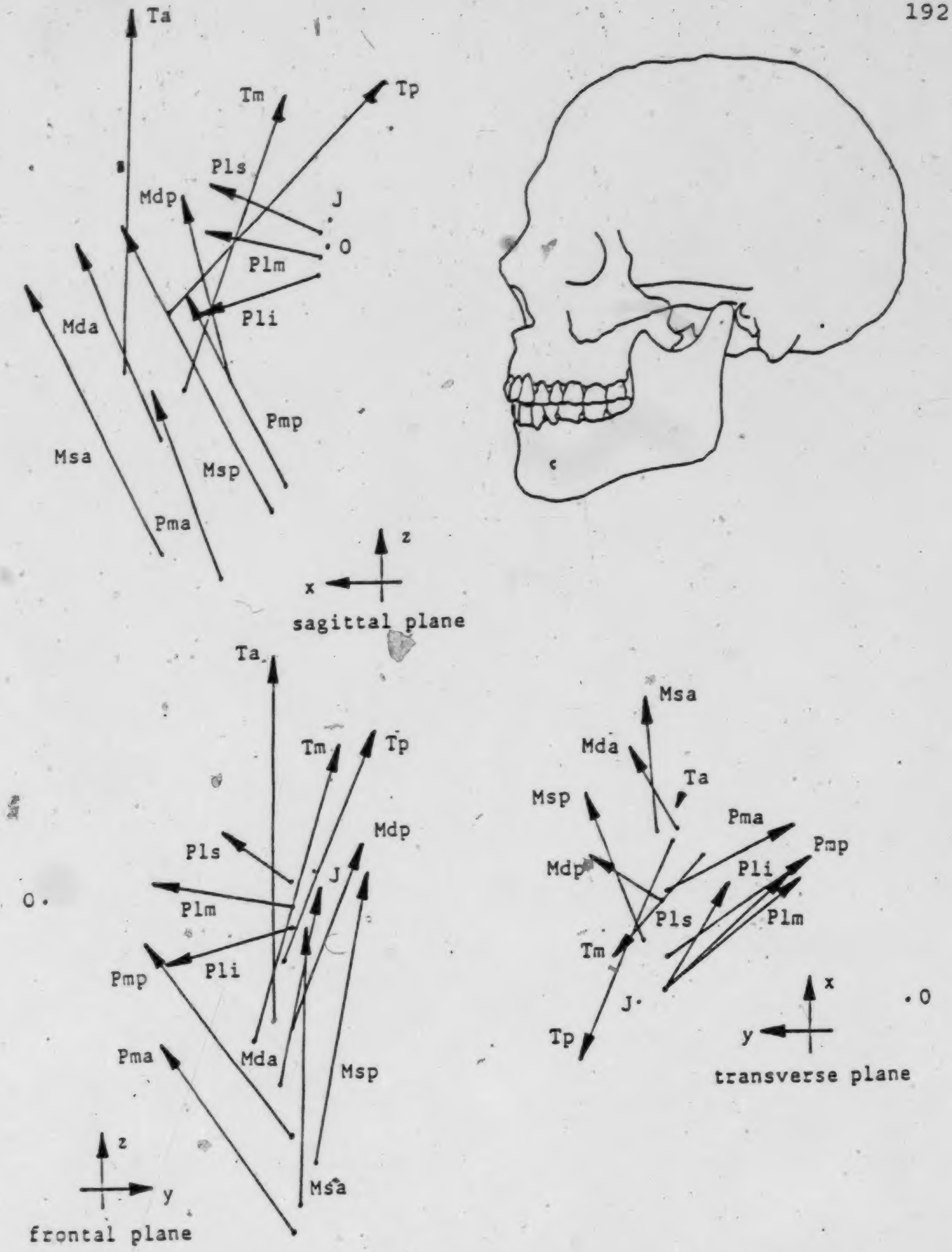
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Fig. 10 The directions of the muscle parts for the Amerindian (AI). Abbreviations are in Table 2. O, the origin of the coordinate system; J, the position of the joint reaction force.

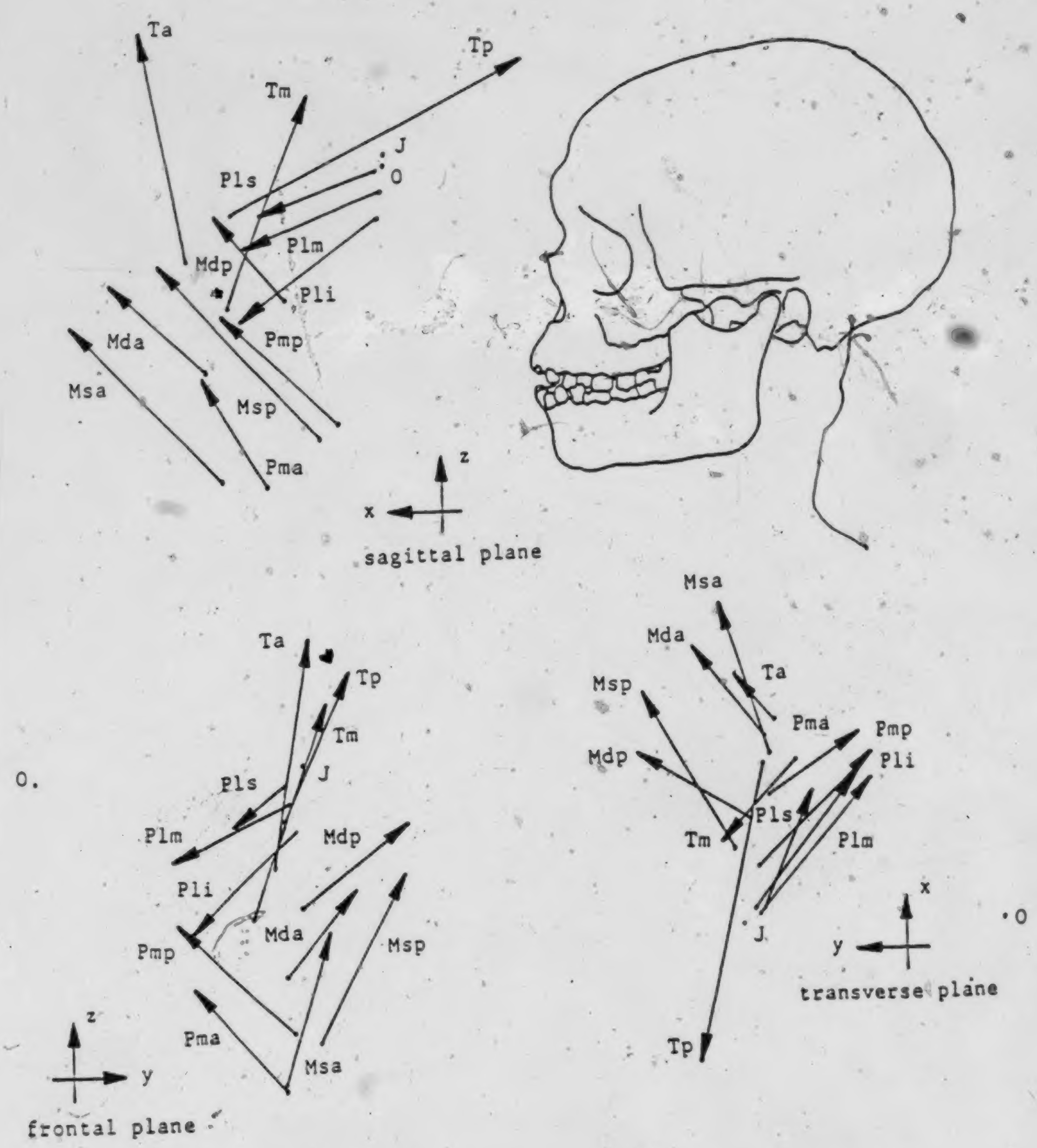
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Fig. 11 The directions of the muscle parts for the Australian Aborigine (AA). Abbreviations are in Table 2. O, the origin of the coordinate system; J, the position of the joint reaction force.

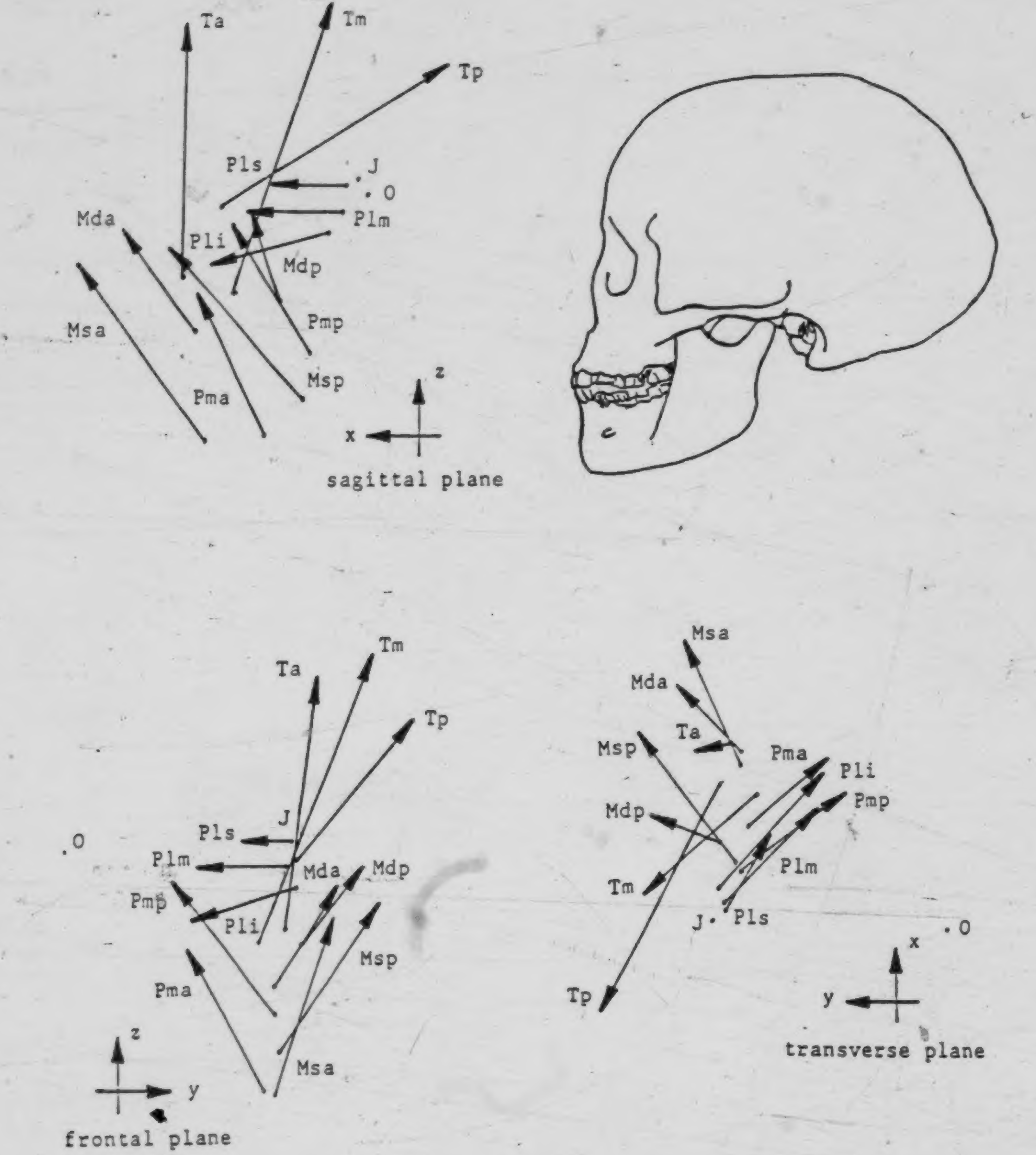
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Fig. 12 The directions of the muscle parts for the Bushman (BM). Abbreviations are in Table 2. O, the origin of the coordinate system; J, the position of the joint reaction force.

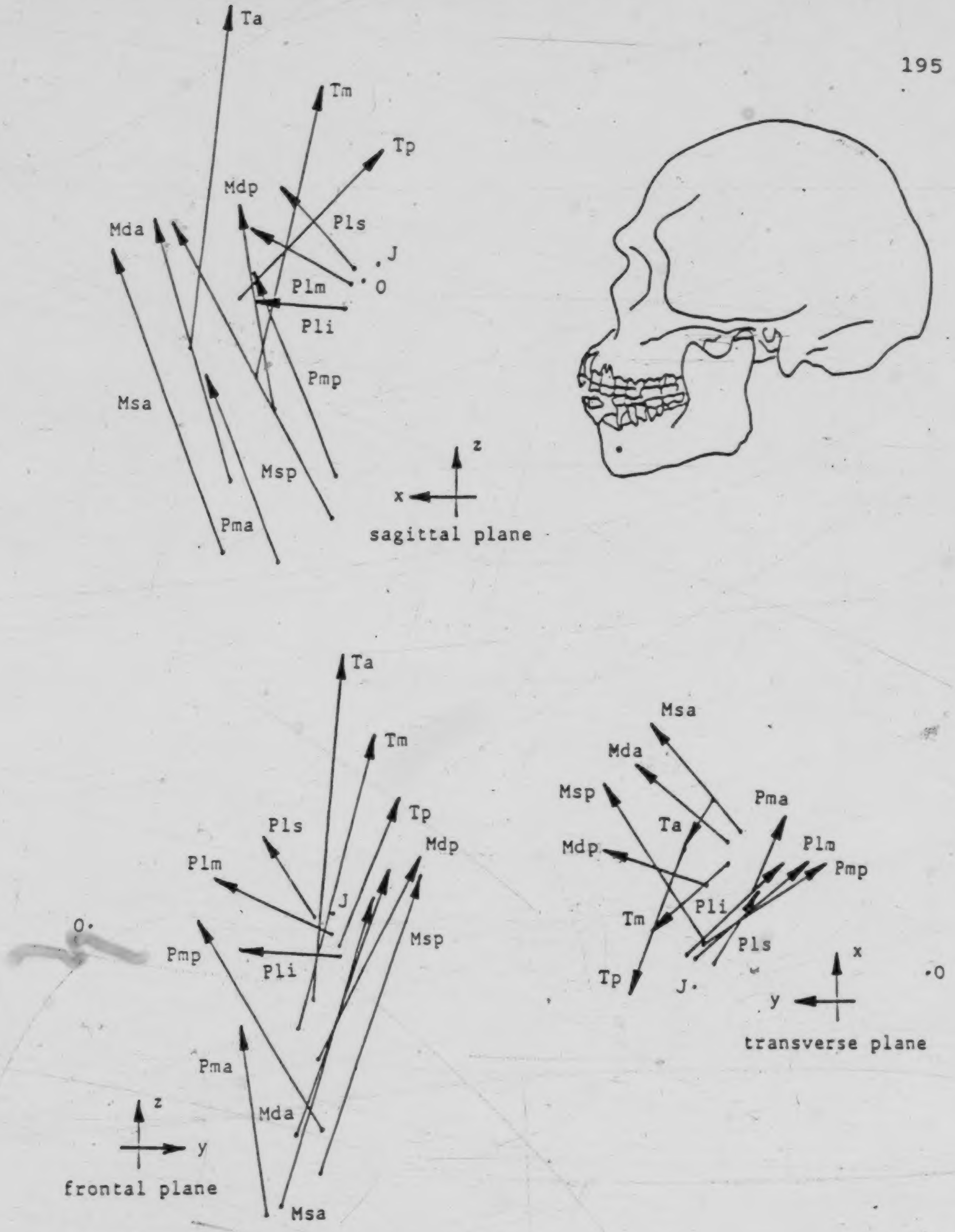
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Fig. 13 The directions of the muscle parts for the Skhul V Hominid (SV). Abbreviations are in Table 2. O, the origin of the coordinate system; J, the position of the joint reaction force.

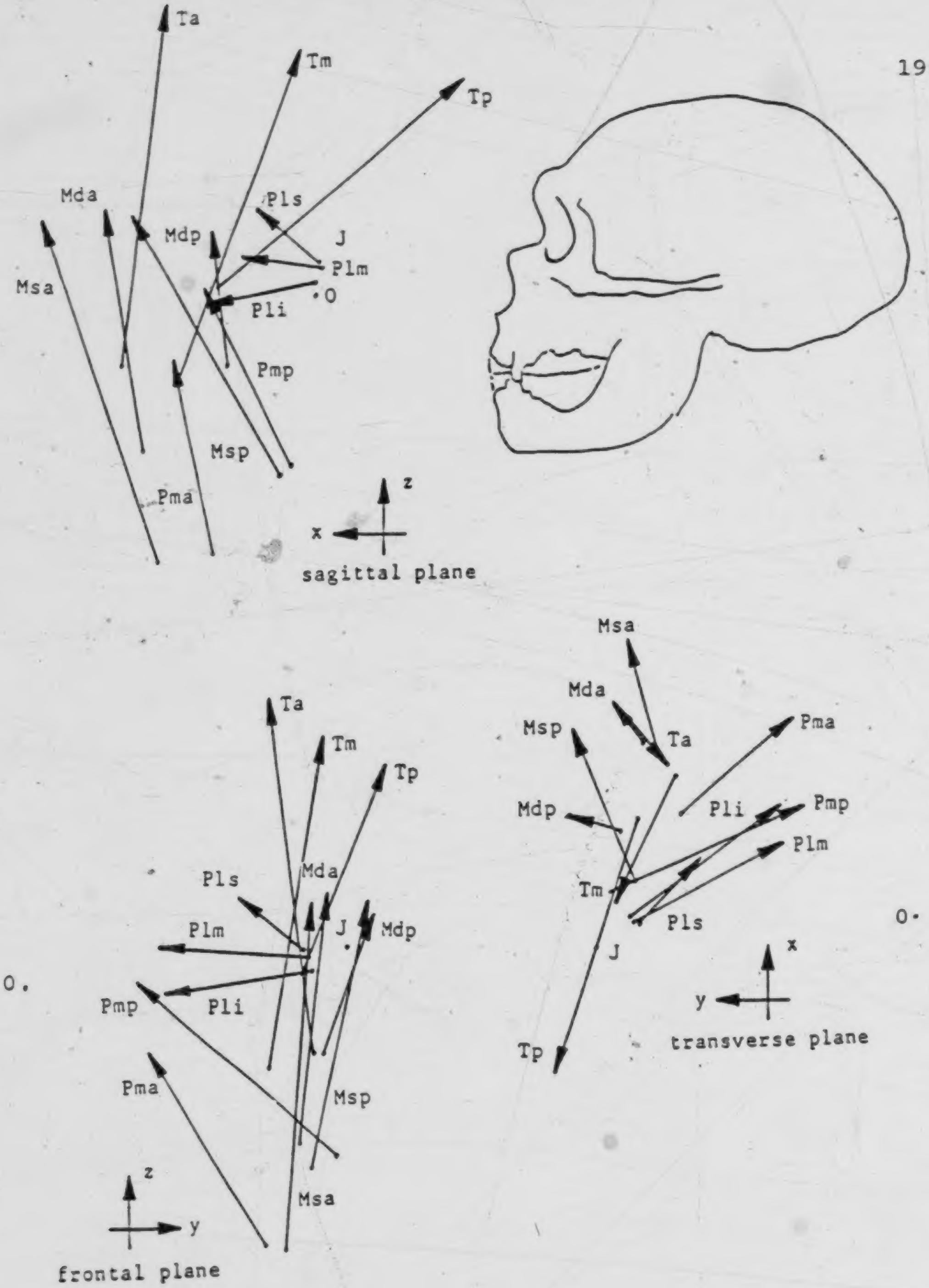
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Fig. 14 The directions of the muscle parts for the La Chapelle-aux-Saints Hominid (CS). Abbreviations are in Table 2. O, the origin of the coordinate system; J, the position of the joint reaction force.

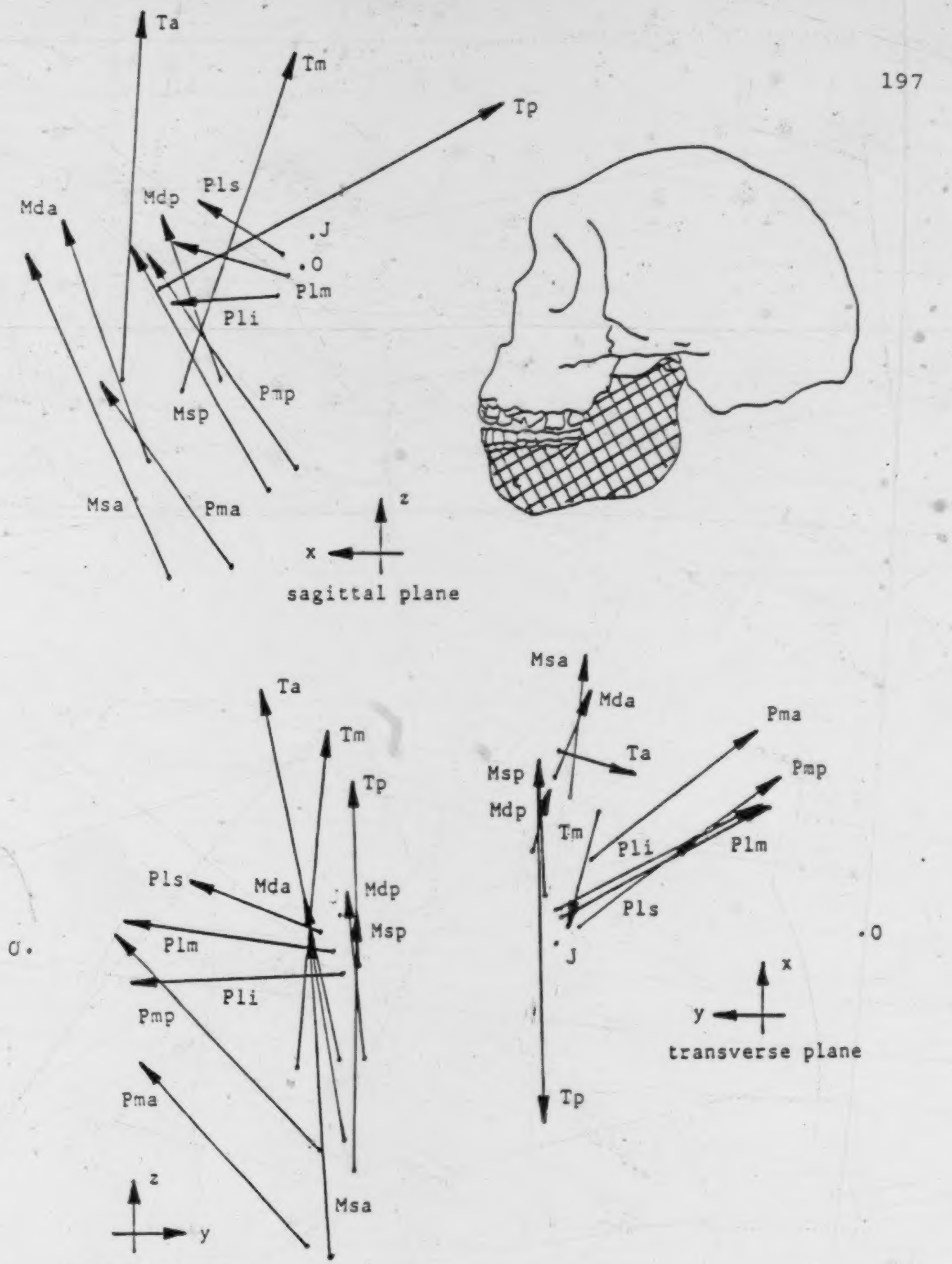
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Fig. 15 The directions of the muscle parts for Rhodesian Man (RM). Abbreviations are in Table 2. O, the origin of the coordinate system; J, the position of the joint reaction force. Cranium and mandible are from different individuals.

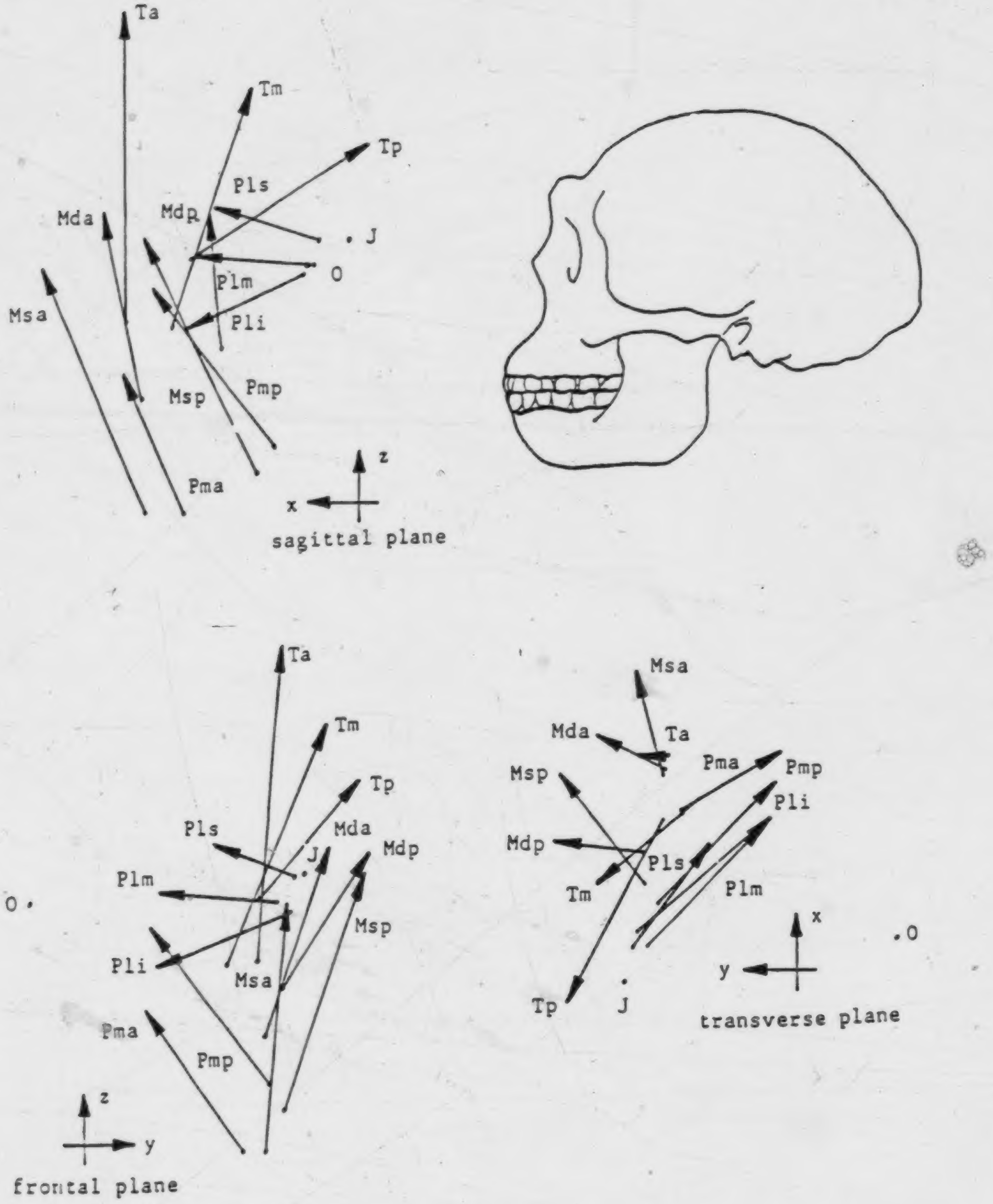
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Fig. 16 The directions of the muscle parts for Peking Man (PM). Abbreviations are in Table 2. O, the origin of the coordinate system; J, the position of the joint reaction force.

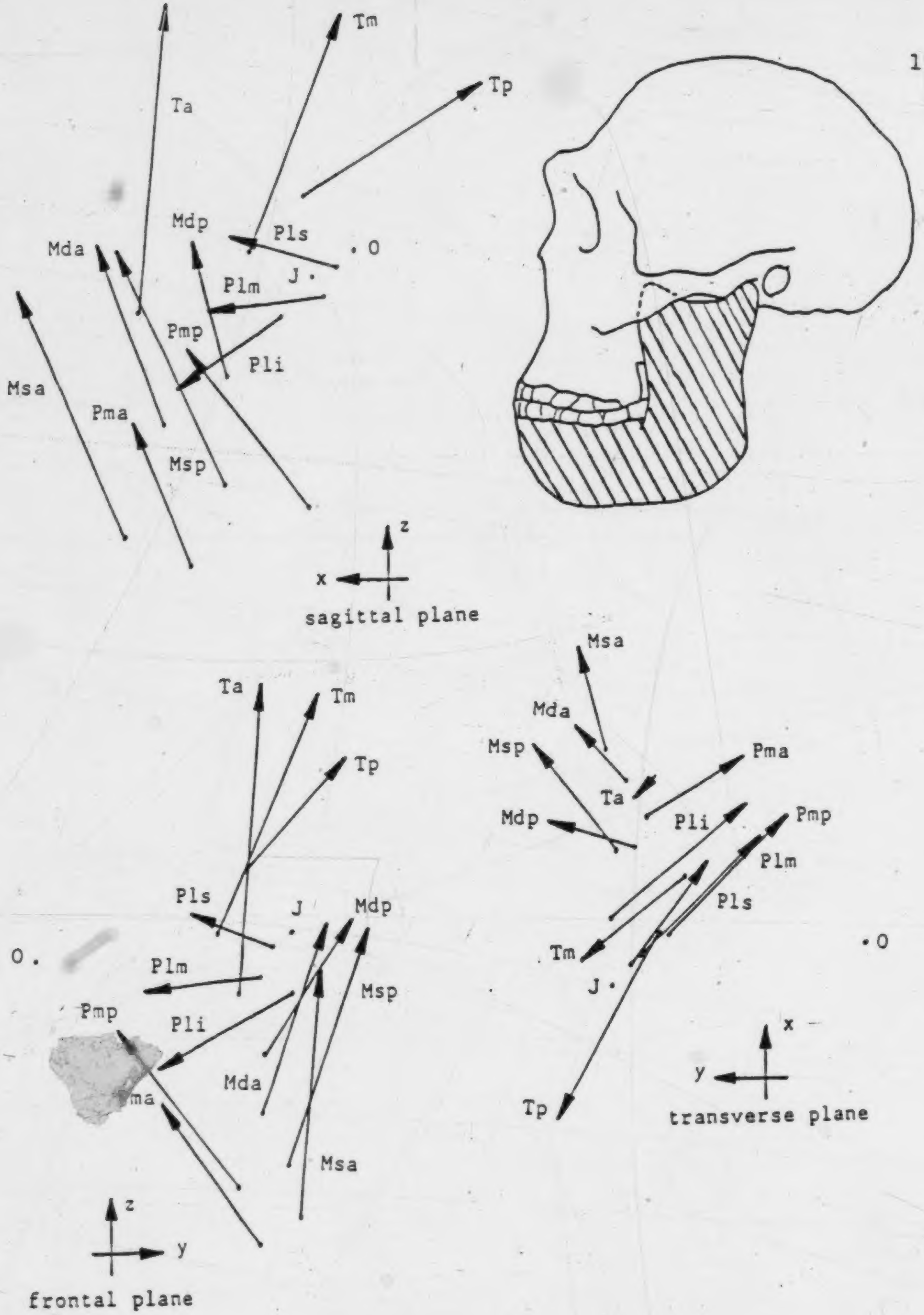
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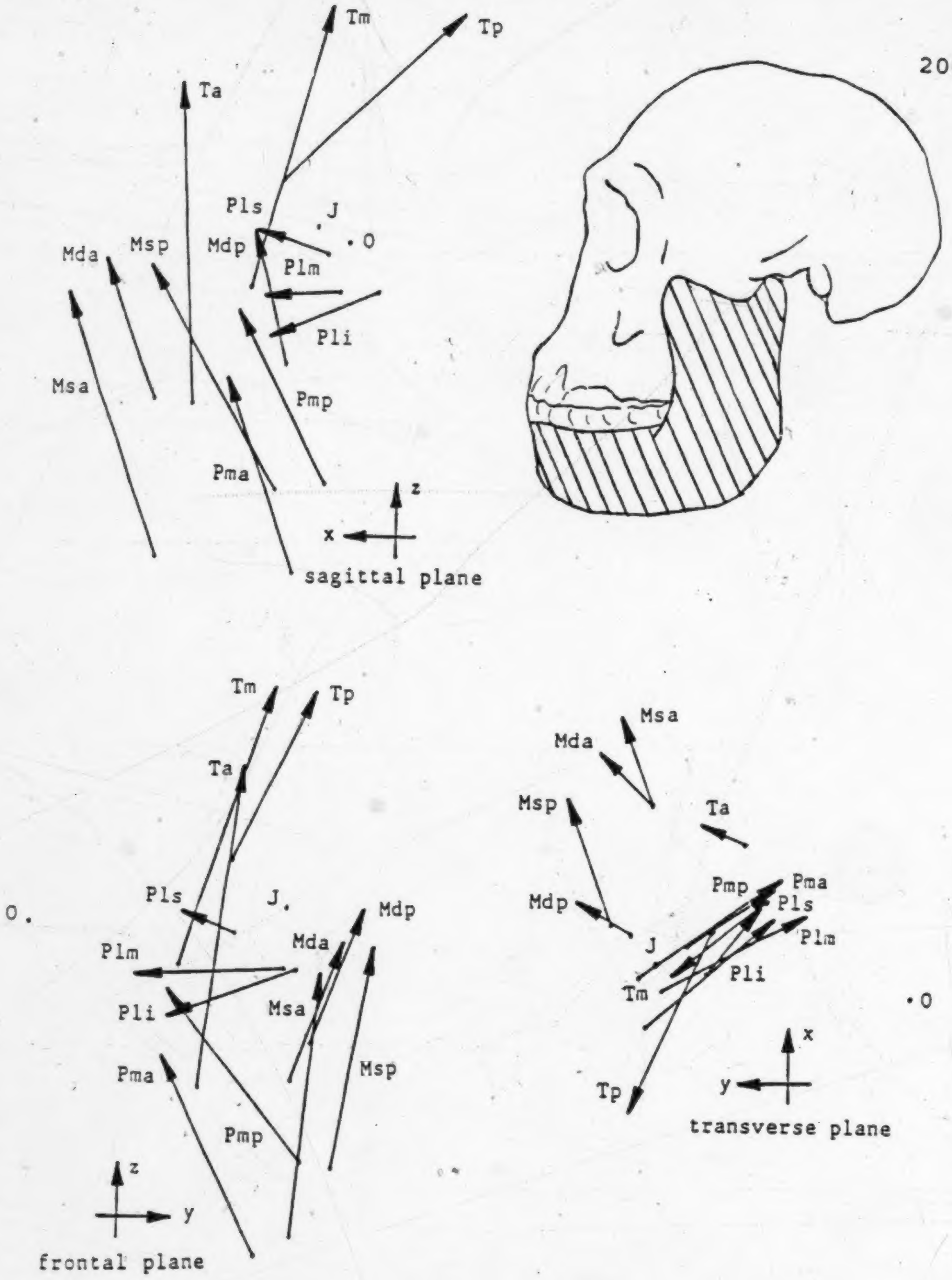
Fig. 17 The directions of the muscle parts for the African Erectus (AE). Abbreviations are in Table 2. O, the origin of the coordinate system; J, the position of the joint reaction force. The mandible is hypothetical.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J
Plm
Pli
Tm
O
x
y
Tp
transverse plane

Fig. 18 The directions of the muscle parts for Habiline Hominid 2 (H2). Abbreviations are in Table 2. O, the origin of the coordinate system; J, the position of the joint reaction force. The mandible is hypothetical.

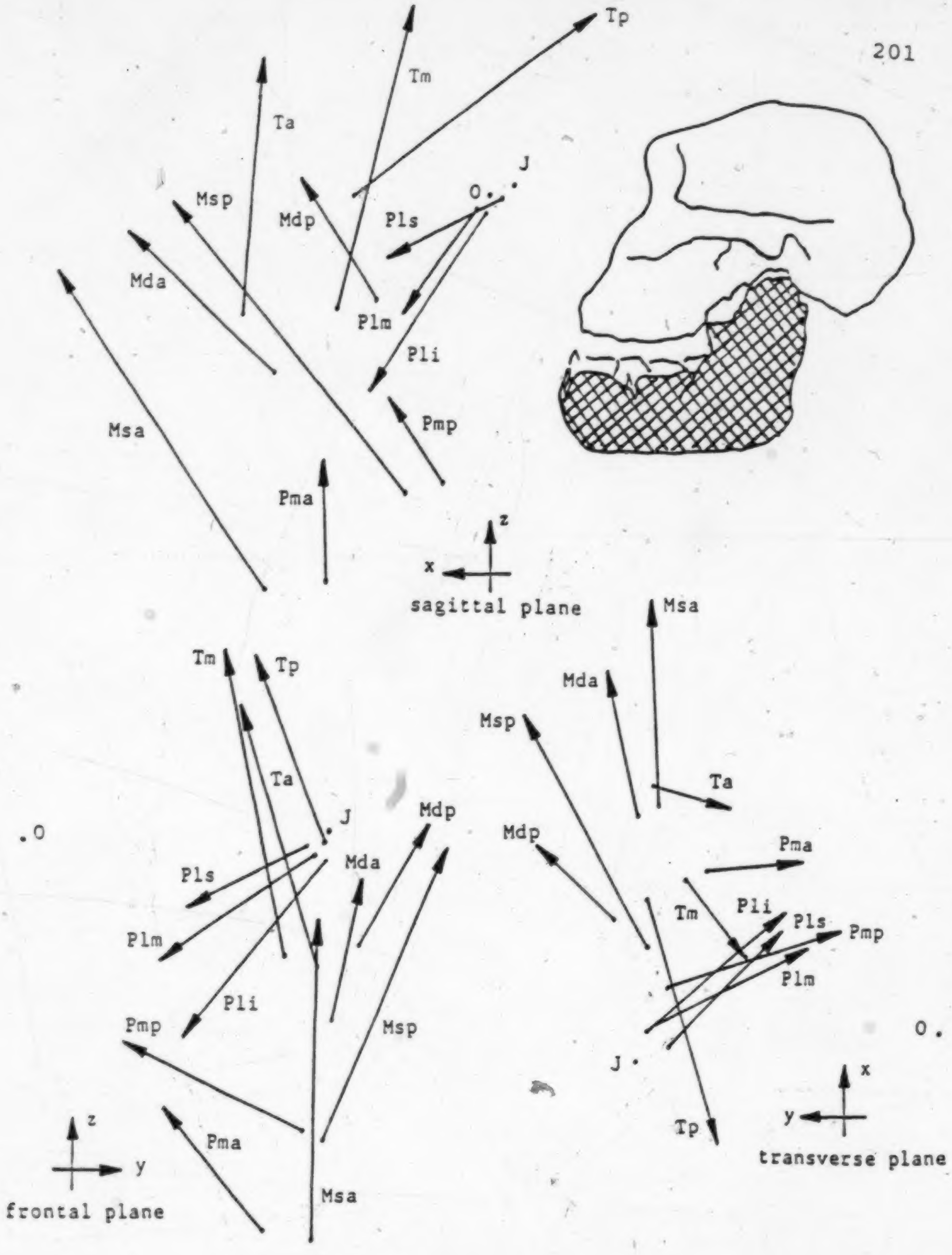

Tp
Tm
Ta
J
O
Msp
Mdp
Pls
Mda
Plm
Pli
Msa
Pmp
Pma
z
x
sagittal plane
Tm
Tp
Ta
.O
J
Mdp
Pls
Mda
Plm
Pli
Pmp
Msp
Pma
Msa
z
y
frontal plane
Msa
Mda
Msp
Ta
Mdp
Pma
Tm
Pli
Pls
Pmp
Plm
O.
J
Tp
x
y
transverse plane

Fig. 19 The directions of the muscle parts for the Robust Australopithecine (RA). Abbreviations are in Table 2. O, the origin of the coordinate system; J, the position of the joint reaction force. Cranium and mandible are from different individuals.

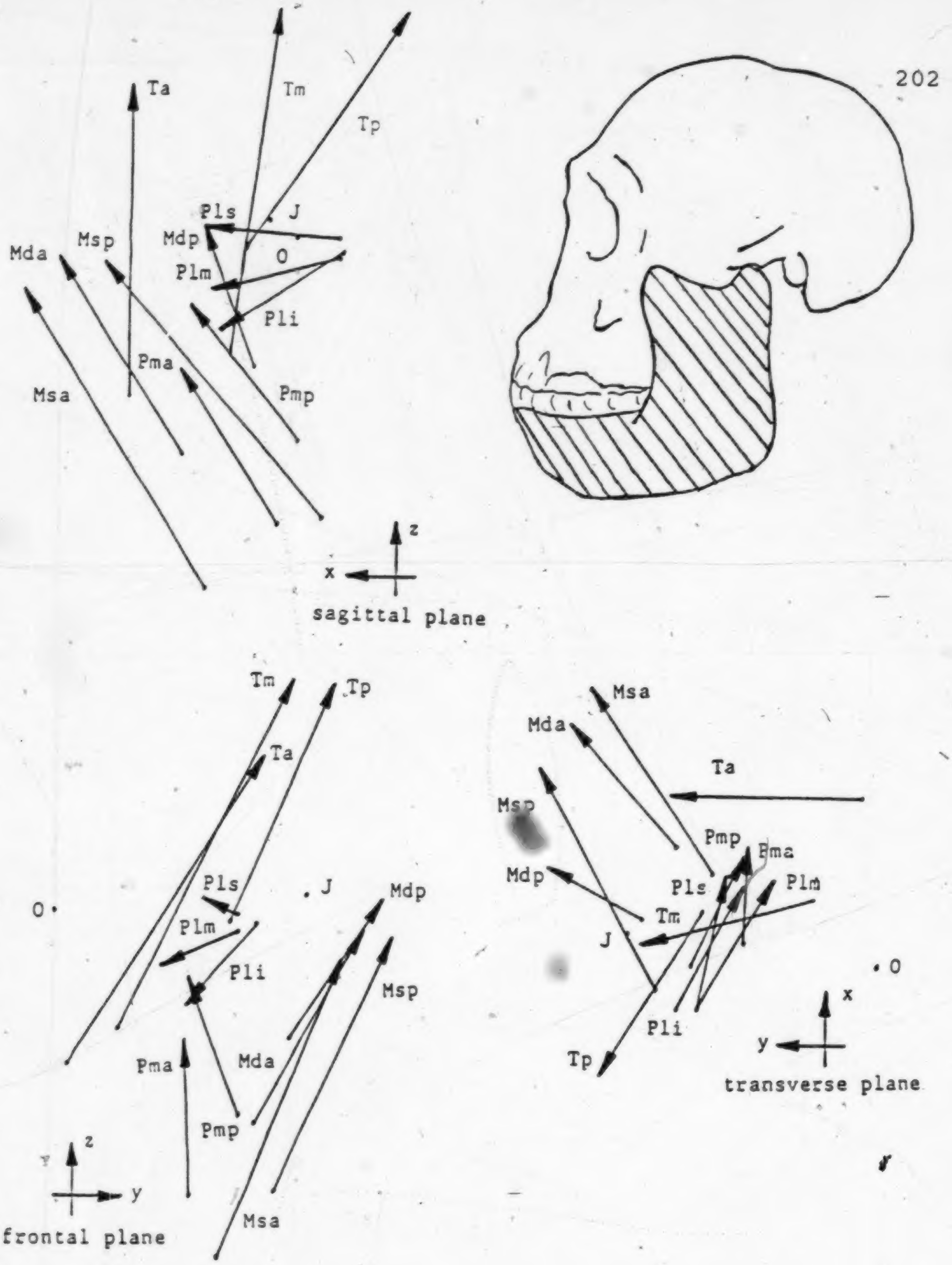
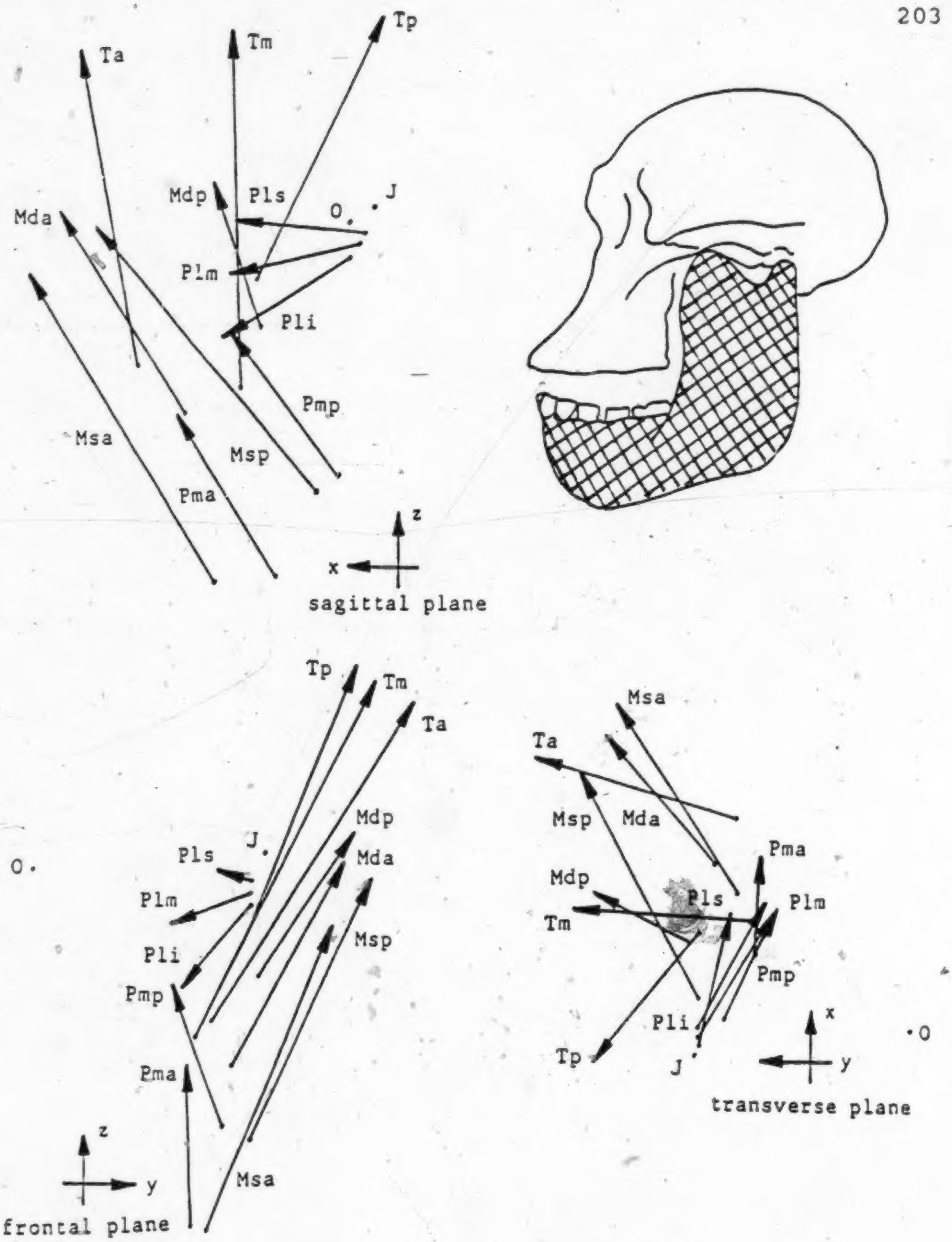

Ta
Tm
Tp
Pls
J
Mdp
Mda
Msp
O
Plm
Pli
Pma
Msa
Pmp
z
x
sagittal plane
Tm
Tp
Ta
Pls
J
Mdp
O
Plm
Pli
Msp
Pma
Mda
Pmp
Msa
z
y
frontal plane
Msa
Mda
Ta
Msp
Pmp
Pma
Mdp
Pls
Plm
Tm
J
O
Pli
Tp
x
y
transverse plane

Fig. 20 The directions of the muscle parts for Habiline Hominid 1 (H1). Abbreviations are in Table 2. O, the origin of the coordinate system; J, the position of the joint reaction force. The mandible is hypothetical.


Ta
Tm
Tp
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Pls
O.
J
Mda
Plm
Pli
Pmp
Msa
Msp
Pma
z
x
sagittal plane
Tp
Tm
Ta
Mdp
Mda
J.
Pls
O
Plm
Pli
Msp
Pmp
Pma
z
y
Msa
frontal plane
Msa
Ta
Msp
Mda
Pma
Mdp
Pls
Plm
Tm
Pmp
Pli
x
O
Tp
J
y
transverse plane

Fig. 21 The directions of the muscle parts for the Gracile Australopithecine (GA). Abbreviations are in Table 2. O, the origin of the coordinate system; J, the position of the joint reaction force. Cranium and mandible are from different individuals.

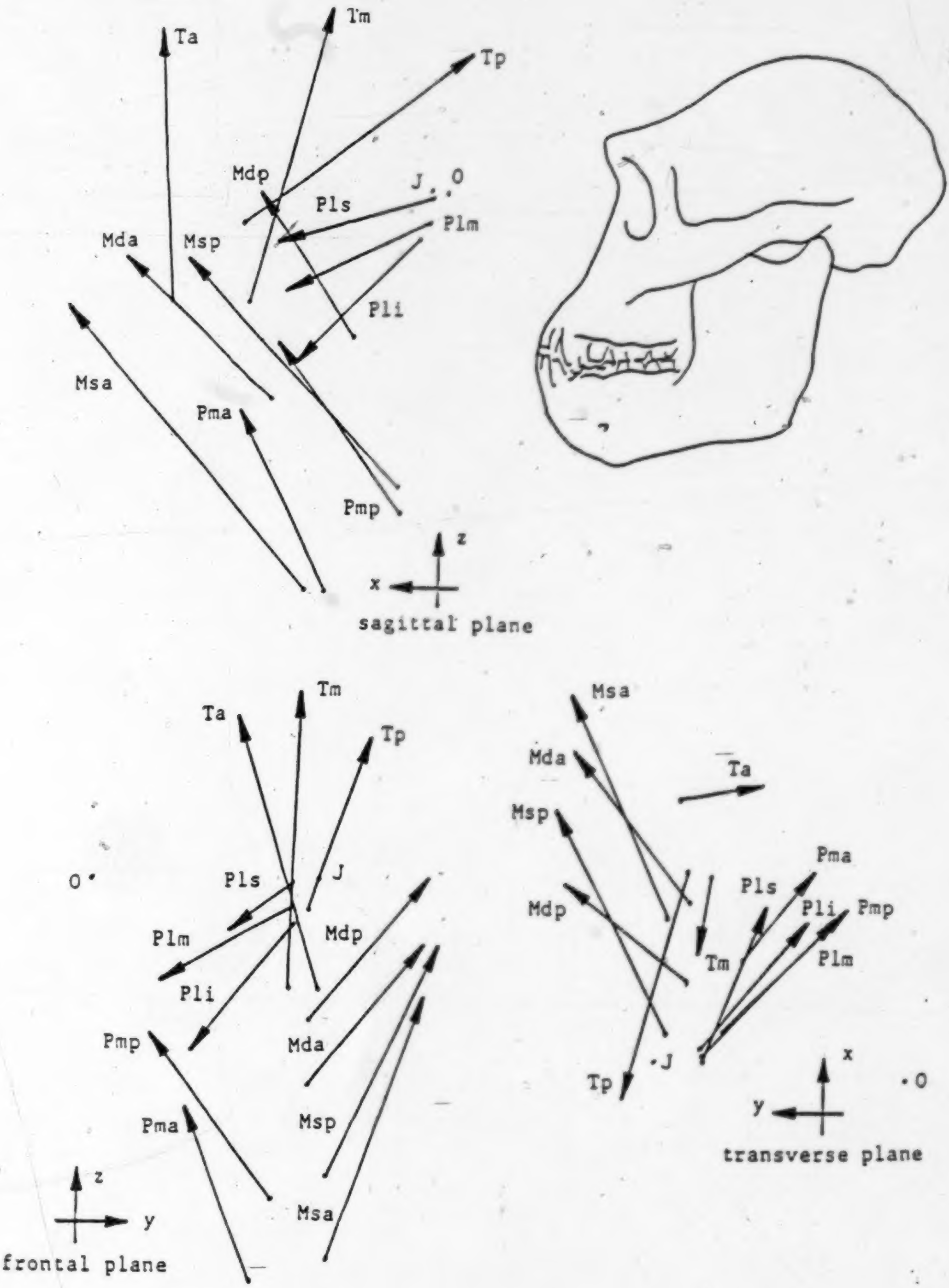

Ta
Tm
Tp
Mdp
J
O
Pls
Plm
Mda
Msp
Pli
Msa
Pma
Pmp
z
x
sagittal plane
Ta
Tm
Tp
O
Pls
J
Plm
Mdp
Pli
Pmp
Mda
Pma
Msp
Msa
z
y
frontal plane
Msa
Mda
Ta
Msp
Pma
Pls
Pli
Pmp
Mdp
Tm
Plm
J
Tp
x
O
y
transverse plane

Fig. 22 The directions of the muscle parts for the Afar Hominid (AH). Abbreviations are in Table 2. O, the origin of the coordinate system; J, the position of the joint reaction force.

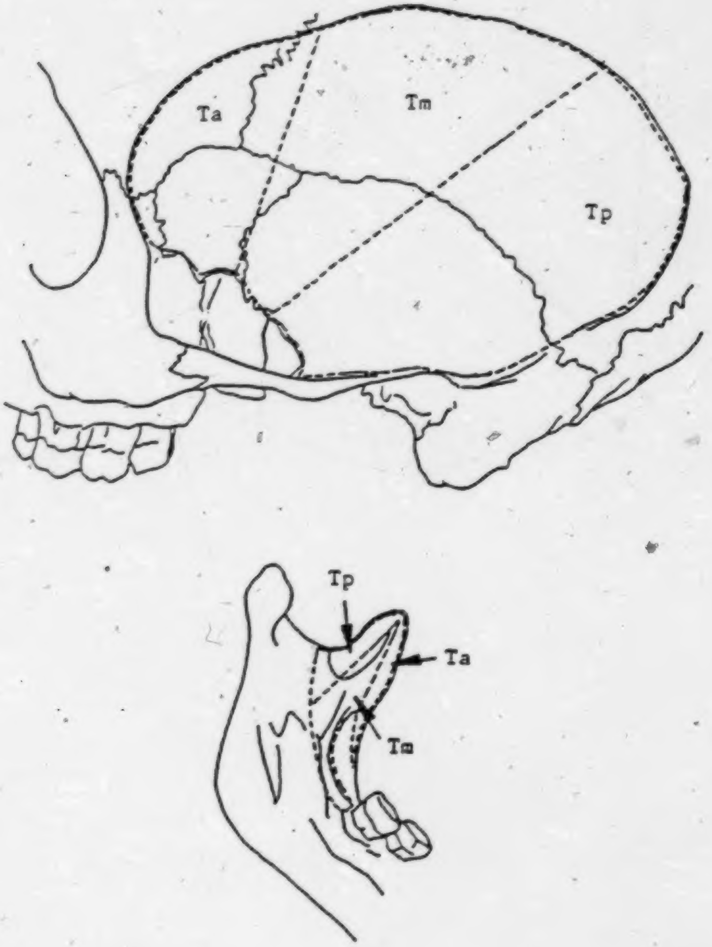


Fig. 23 Lateral view of the cranium (above) and medial view of the mandibular ramus (below) showing the attachment areas of the parts of the temporalis muscle. See Table 2 for abbreviations.

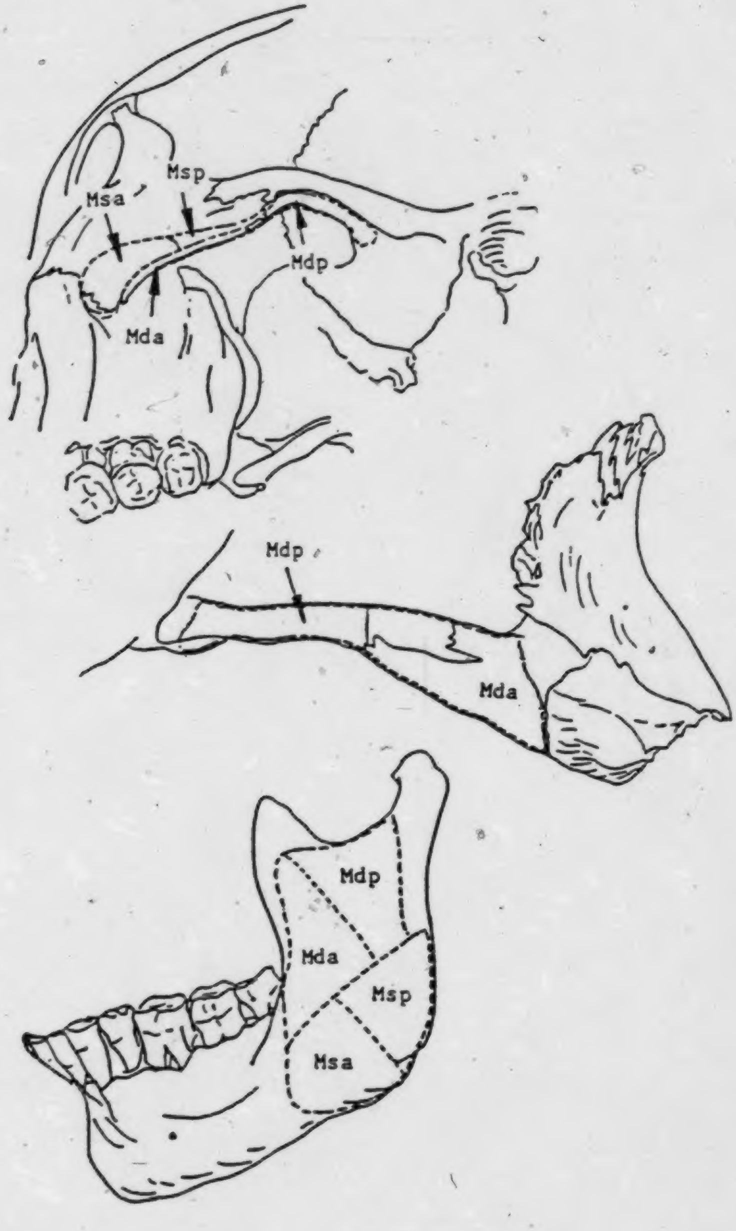
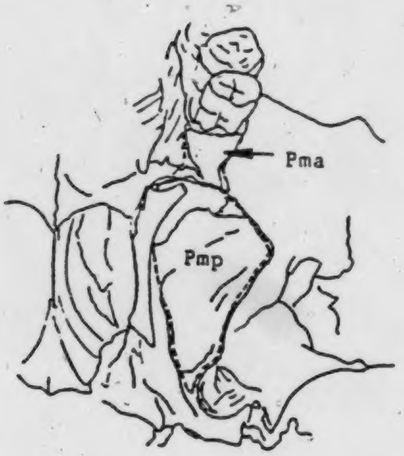

Msp
Msa
Mdp
Mda
Mdp
Mda
Mdp
Mda
Msp
Msa

Fig. 24 Oblique view of the zygomatic arch (above), medial view of the arch (middle) and lateral view of the mandibular ramus (below) showing the attachment areas of the parts of the masseter muscle.



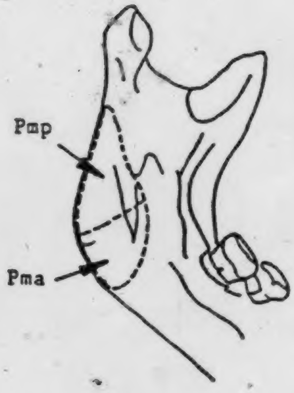


Fig. 25 Inferoposterior view of the pterygoid plates (above) and medial view of the mandibular ramus (below) showing the attachment areas of the parts of the medial pterygoid muscle.

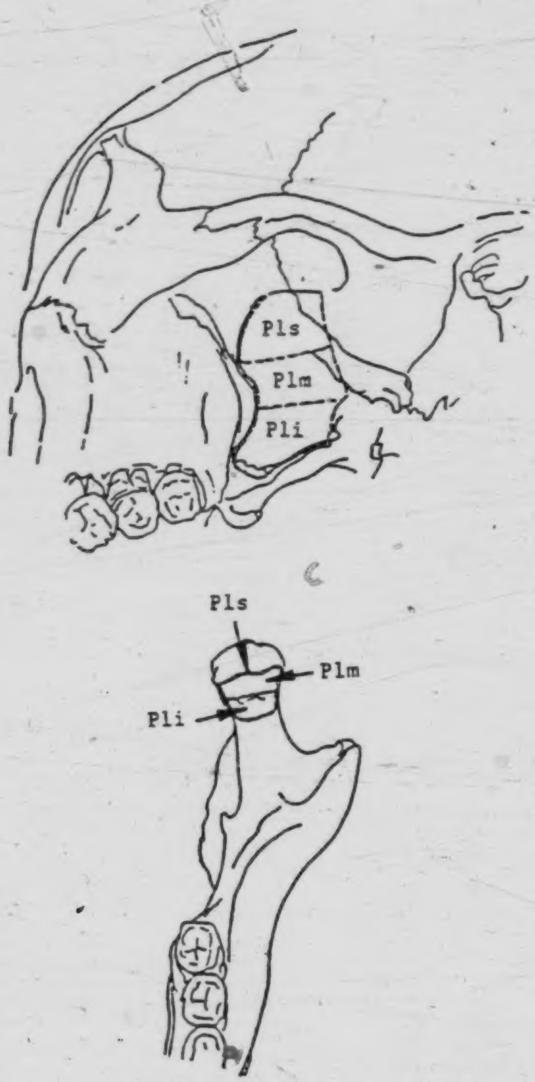

Pls
Plm
Pli
Pls
Plm
Pli

Fig. 26 Oblique view of the sphenoid bone (above) and anterior view of the mandibular condyle (below) showing the attachment areas of the parts of the lateral pterygoid muscle.

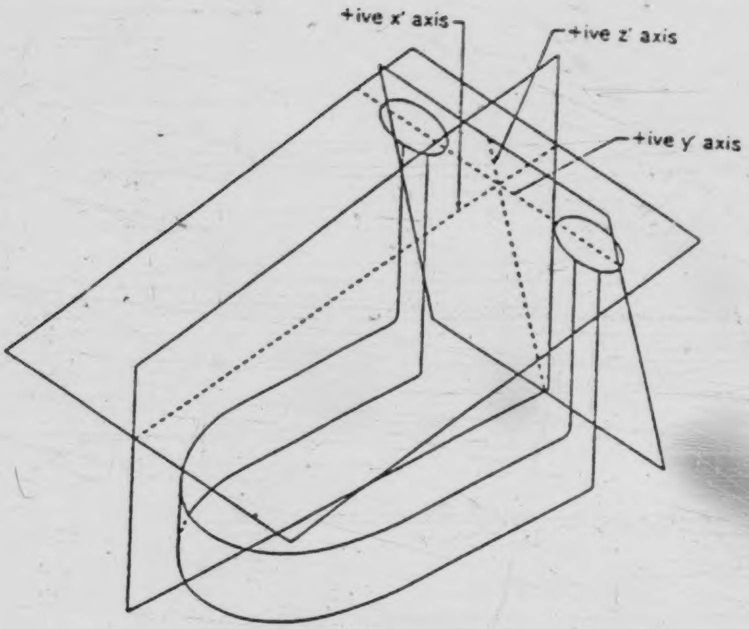


Fig. 27 The planes of the coordinate system in relation to a stylized mandible. The origin was in the sagittal plane, at the midpoint of a straight line joining the centers of the two condyles (found in this study by viewing them from the side). The xz plane was the sagittal plane. The xy plane was parallel to the averaged occlusal plane and contained the centers of the two condyles. The averaged occlusal plane was defined by three points - the midpoint between the central incisors at the level of their occlusal surfaces, and the most posterior points on the occlusal surface of the third molars (provided they showed evidence of use). The yz plane was perpendicular to the other two and also contained the centers of the two condyles.

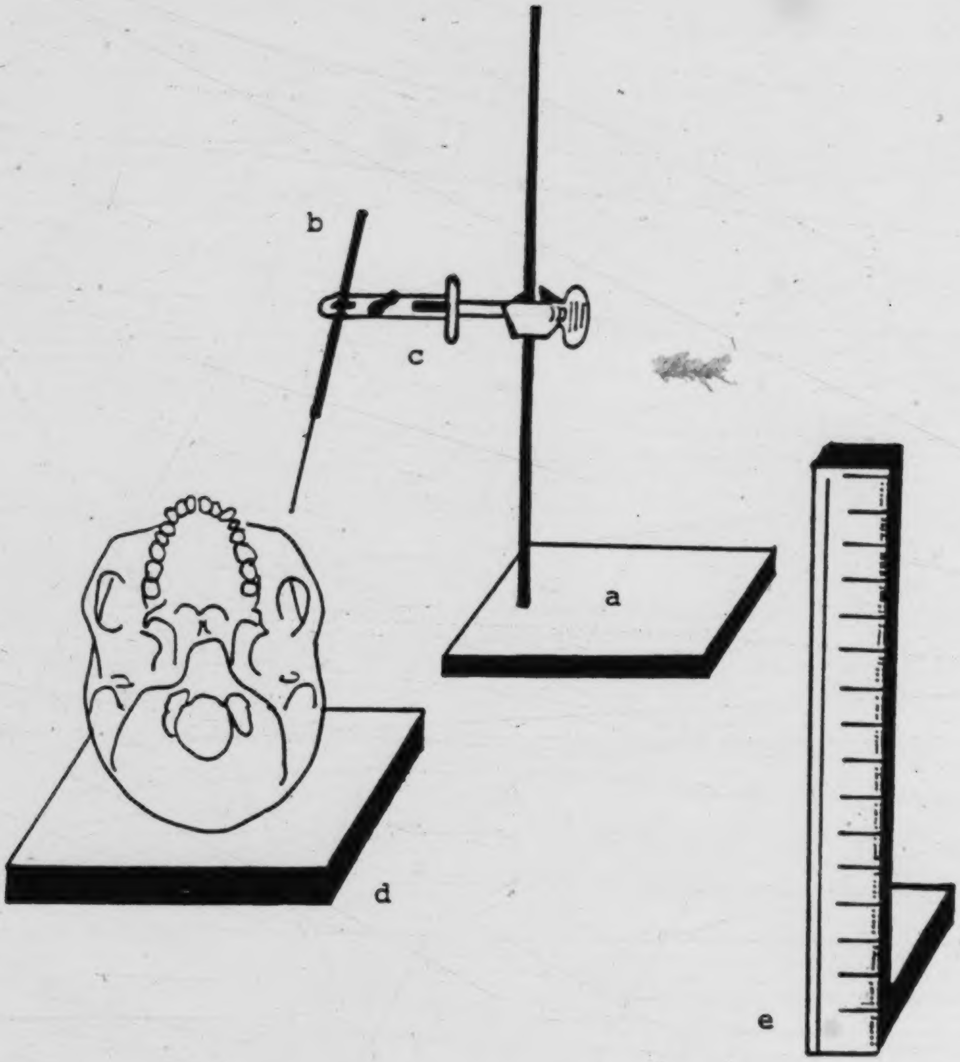


Fig. 28 The measuring tools used in the present study. a, laboratory support composed of a flat base and a vertical rod; b, dissecting needle which served as a pointer; c, thermometer clamp which held the pointer and attached to the vertical rod; d, small piece of plywood upon which the crania and mandibles were mounted in position with plasticine; e, 38cm ruler glued to a wooden stand whose face was perpendicular to the table top.

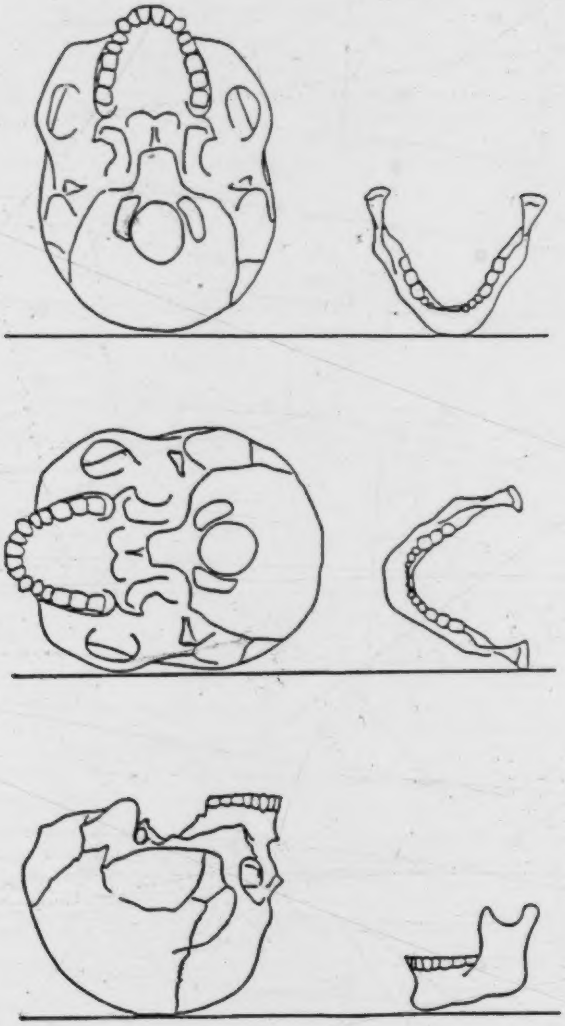


Fig. 29 Positions of the hominid crania and mandibles for measuring x, y and z coordinates. For the x coordinate (top) the intercondylar axis was parallel to the table top and the averaged occlusal plane was perpendicular to it. For the y coordinate (middle) both the intercondylar axis and the averaged occlusal plane were perpendicular to the table top. For the z coordinate (bottom) both the intercondylar axis and the averaged occlusal plane were parallel to the table top.

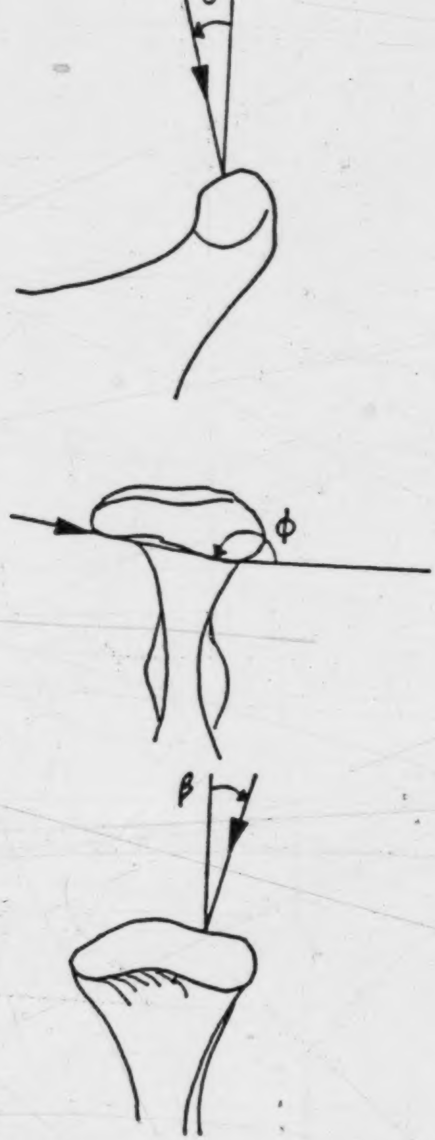


Fig. 30 The direction of the joint reaction force was defined by θ, the angle from the vertical (z) axis, found by dropping a perpendicular to the articular surface, ϕ, the angle in the occlusal plane, found by a line parallel to the long axis of the condyle, and β, the angle by which the condyle slopes in the plane containing the two lines.

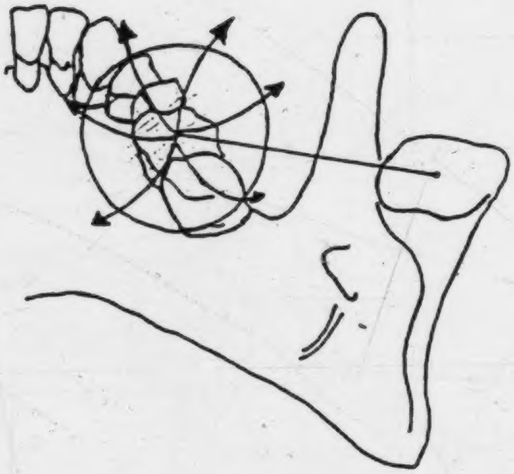


Fig. 31 Because the working side condyle is firmly seated against the articular eminence during biting, a tooth is constrained to move along the surface of a sphere centered at the condyle.

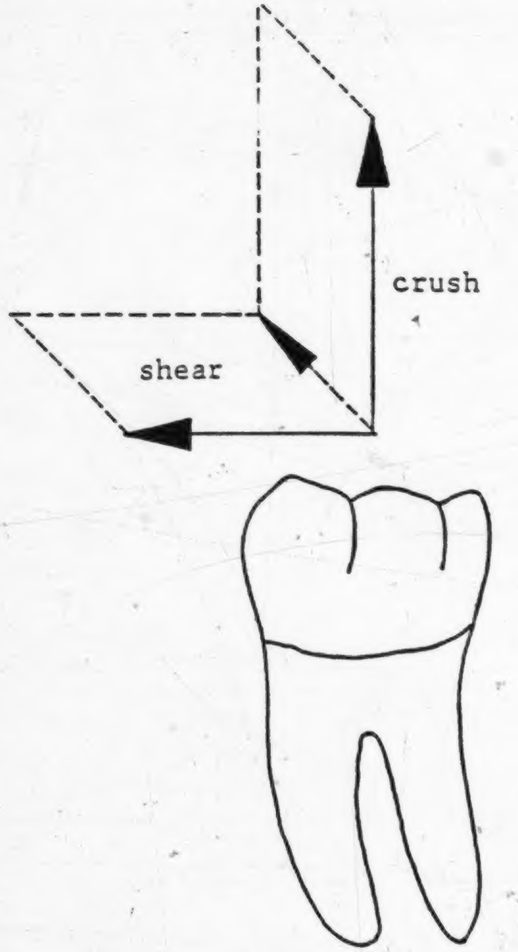

crush
shear

Fig. 32 Crushing and shearing was defined in terms of the movement of the tooth relative to its long axis.

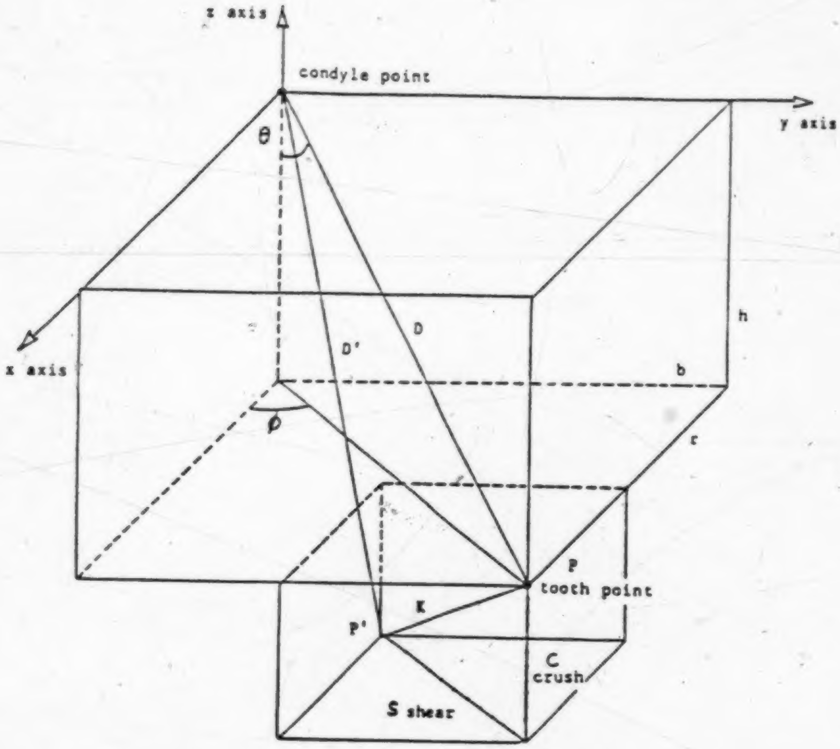


Fig. 33 The geometric model for the calculation of maximum crush:shear (C:S). A tooth on the right side is represented. D, and D', the distance from the condyle to the tooth (constant); P, the position of the tooth in centric occlusion; P', the position of the tooth when the jaw is opened by a distance K (the position from which the jaw is closing); K is set by the investigator and is very small so that it can be modeled as a straight line; θ, the angle between the z axis and D; ϕ, the angle between the x axis and the projection of D in the xy plane; C, the component of crush produced for a given K (the vertical (z) component); S, the component of shear produced for a given K (the vector sum of the horizontal (x) and transverse (y) components). Pure crush exists only in the plane containing P and the z axis (ϕ=0), while pure shear exists only in the plane of ϕ (θ=0). Since a given tooth moves on the surface of a sphere, θ and ϕ change simultaneously as the jaw closes. Maximum crush:shear was determined by first calculating, given K, the minimum value of θ when ϕ=0, then the minimum value of ϕ. The maximum change in these two was thus determined. From these the coordinates of P' were calculated and so the maximum value of the x, y and z components of PP'. These were then translated into maximum crush and shear.

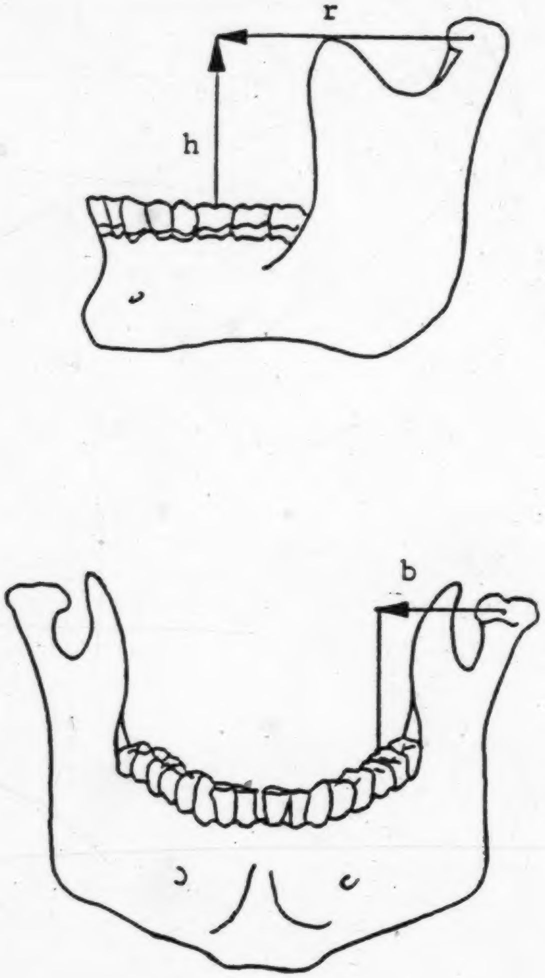


Fig. 34 The position of the condyle with respect to a tooth was measured by h and r in the sagittal plane (above) and b in the frontal plane (below).

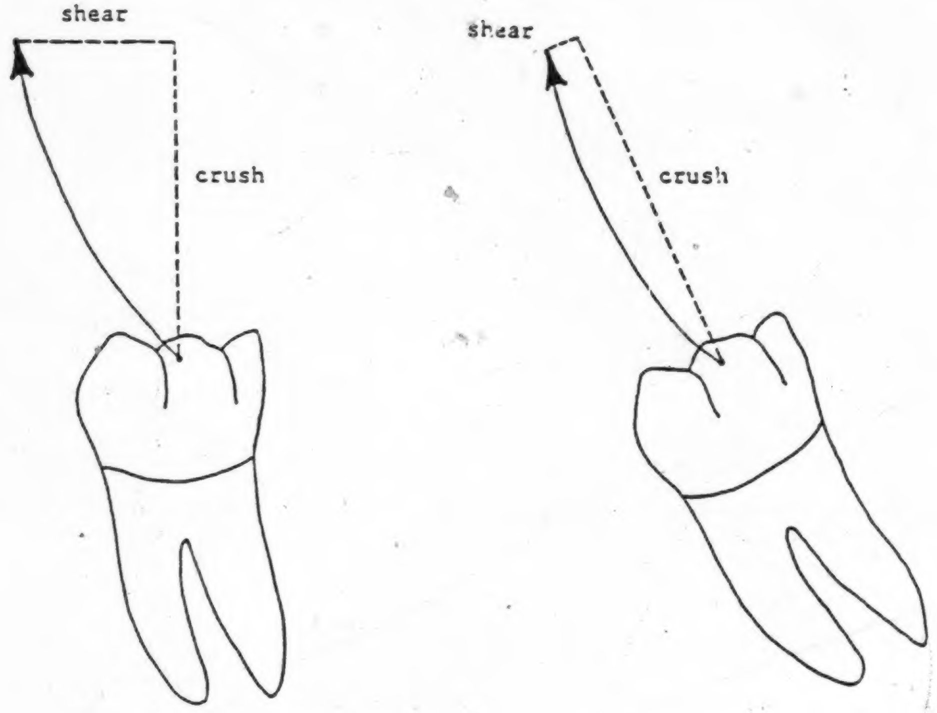


Fig. 35 The effect in the sagittal plane of the orientation of a tooth's long axis to its path of closure on the crush:shear ratio of that tooth. Both teeth have the same h and r, but the tooth on the right is tilted about twenty degrees forward from the vertical. The ratio of crush:shear is considerably improved.

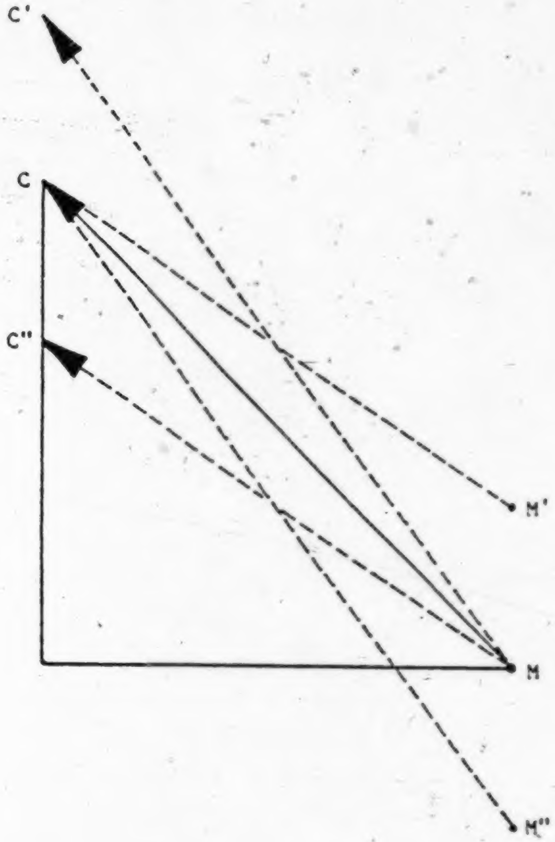


Fig. 36 The direction of a muscle (solid arrow) is determined by the cranial (C) and mandibular (M) attachment points. If the distance between C and M is increased (C to C' or M to M") the component along that axis is increased but the components along the other axes (in three dimensions) are decreased, and vice versa (C to C" or M to M').

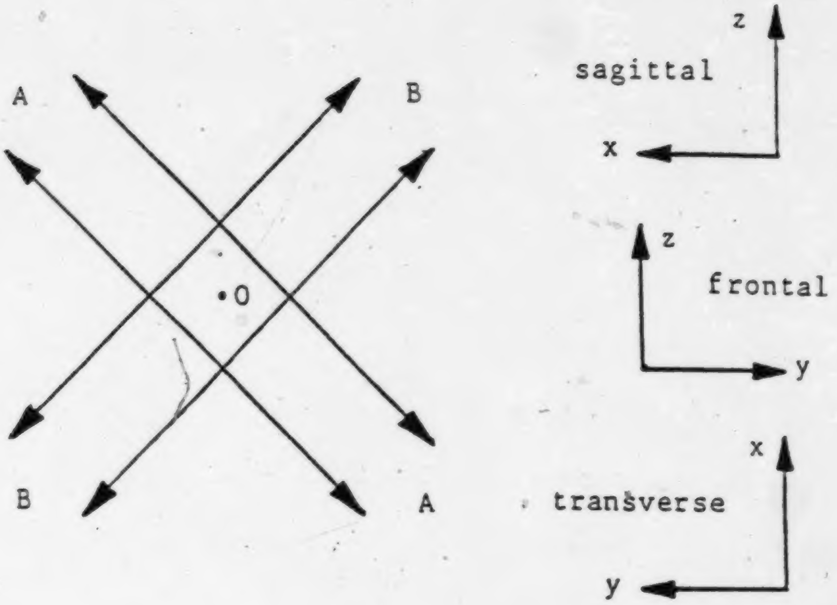


Fig. 37 The length of the moment arm of a muscle is affected by changes in its attachment points. In the sagittal plane, if the line of action of a muscle passes below the point of rotation (the origin, O) and is directed as A, the moment arm is increased when the cranial and/or mandibular attachment points are moved forward and/or downward, but if directed as B, then backward and/or downward. In the frontal plane, if the line of action passes below the origin and is directed as A, the moment arm is increased if the cranial and/or mandibular attachment points are moved inward and/or downward, but if directed as B, then outward and/or downward. Finally, in the transverse plane, if the line of action passes behind the origin and is directed as A, the moment arm is increased if the cranial and/or mandibular attachment points are moved outward and/or backward, but if directed as B, then inward and/or backward.

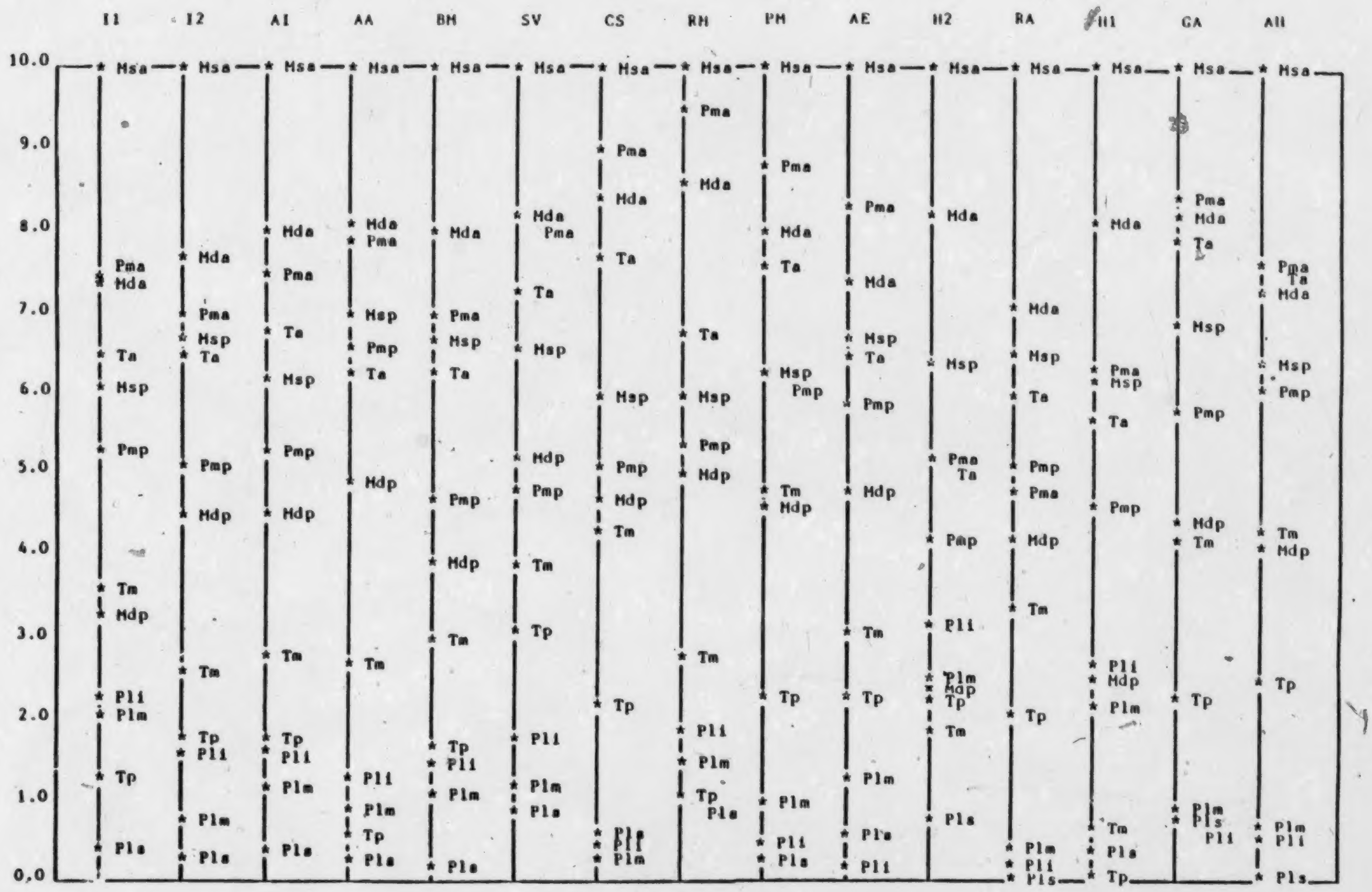


Fig. 38 Relative moment arm lengths of the hominids' muscles.

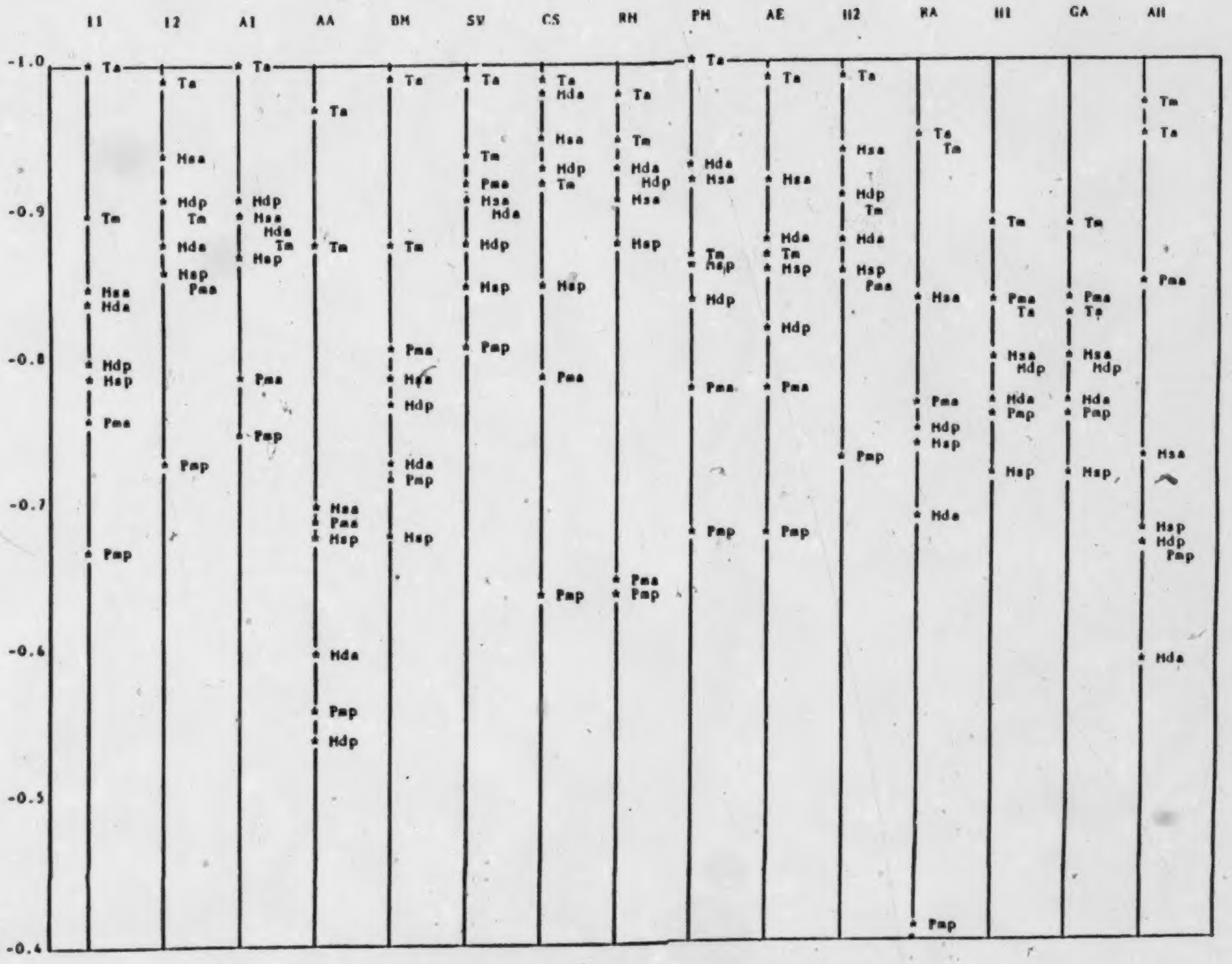


Fig. 39 The components of the hominids' muscles parallel to the vertical bite force.

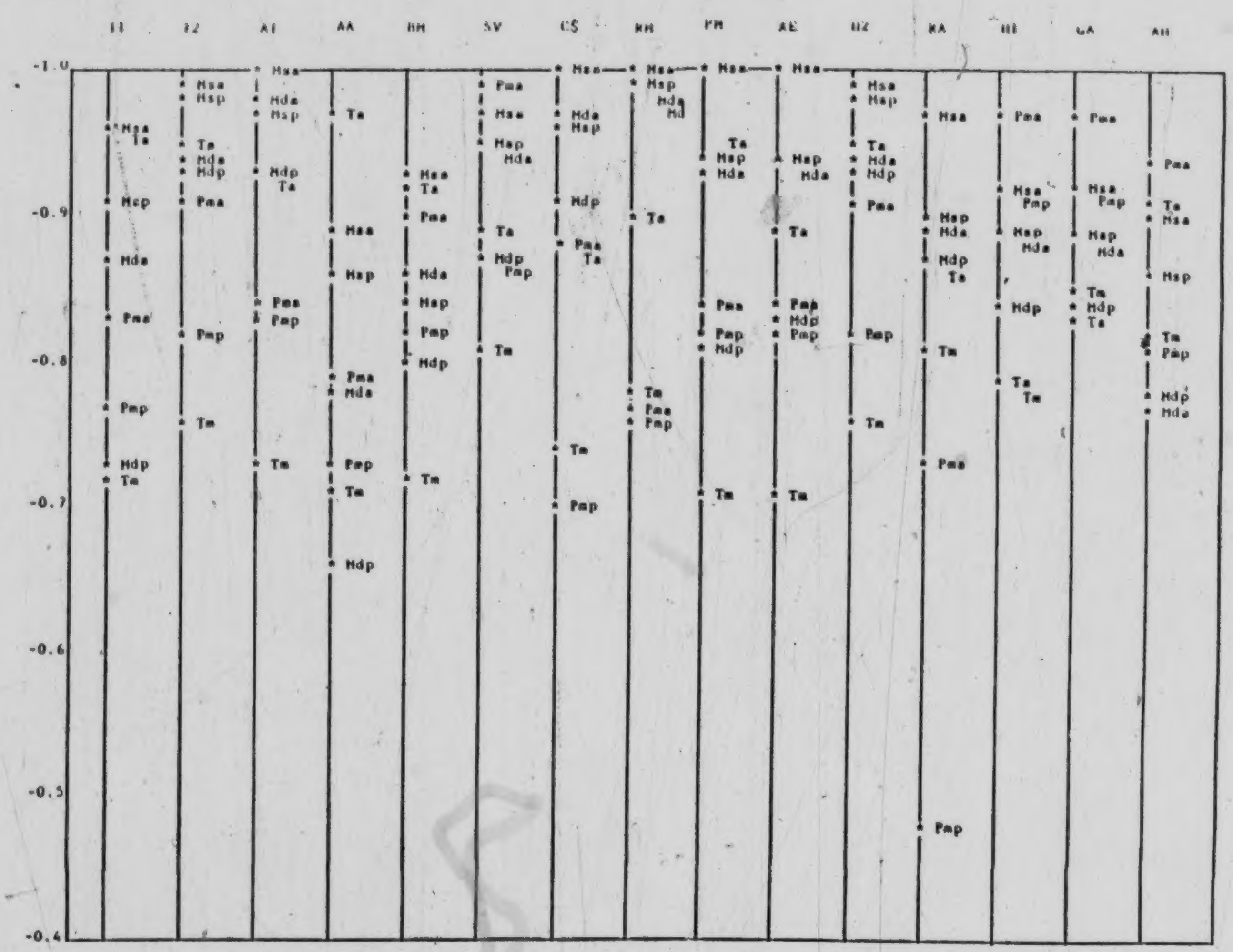


Fig. 40 The components of the hominids' muscles parallel to the anterior bite force.

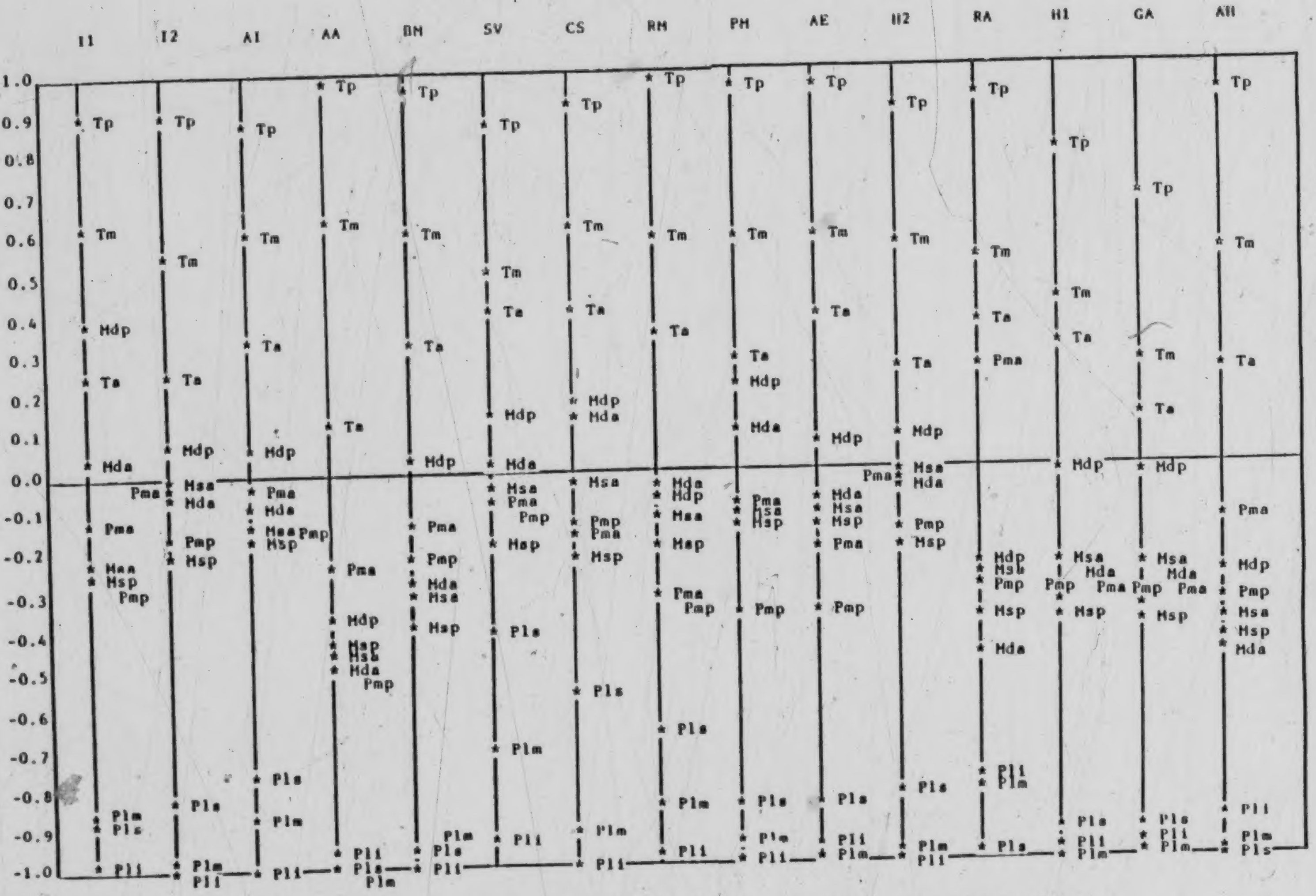


Fig. 41 The components of the hominids' muscles which caused the mandibular condyle to slide on the articular eminence.

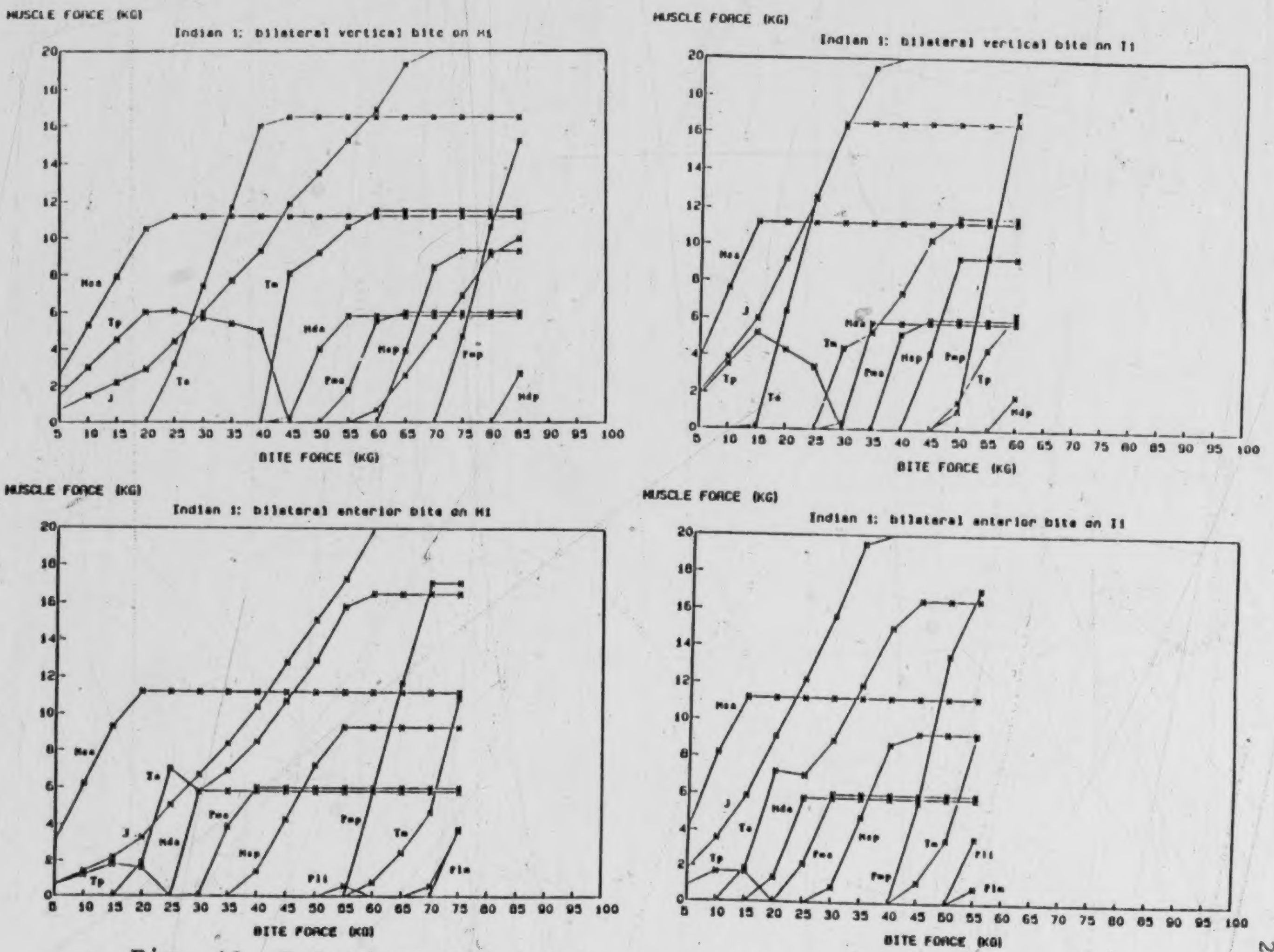
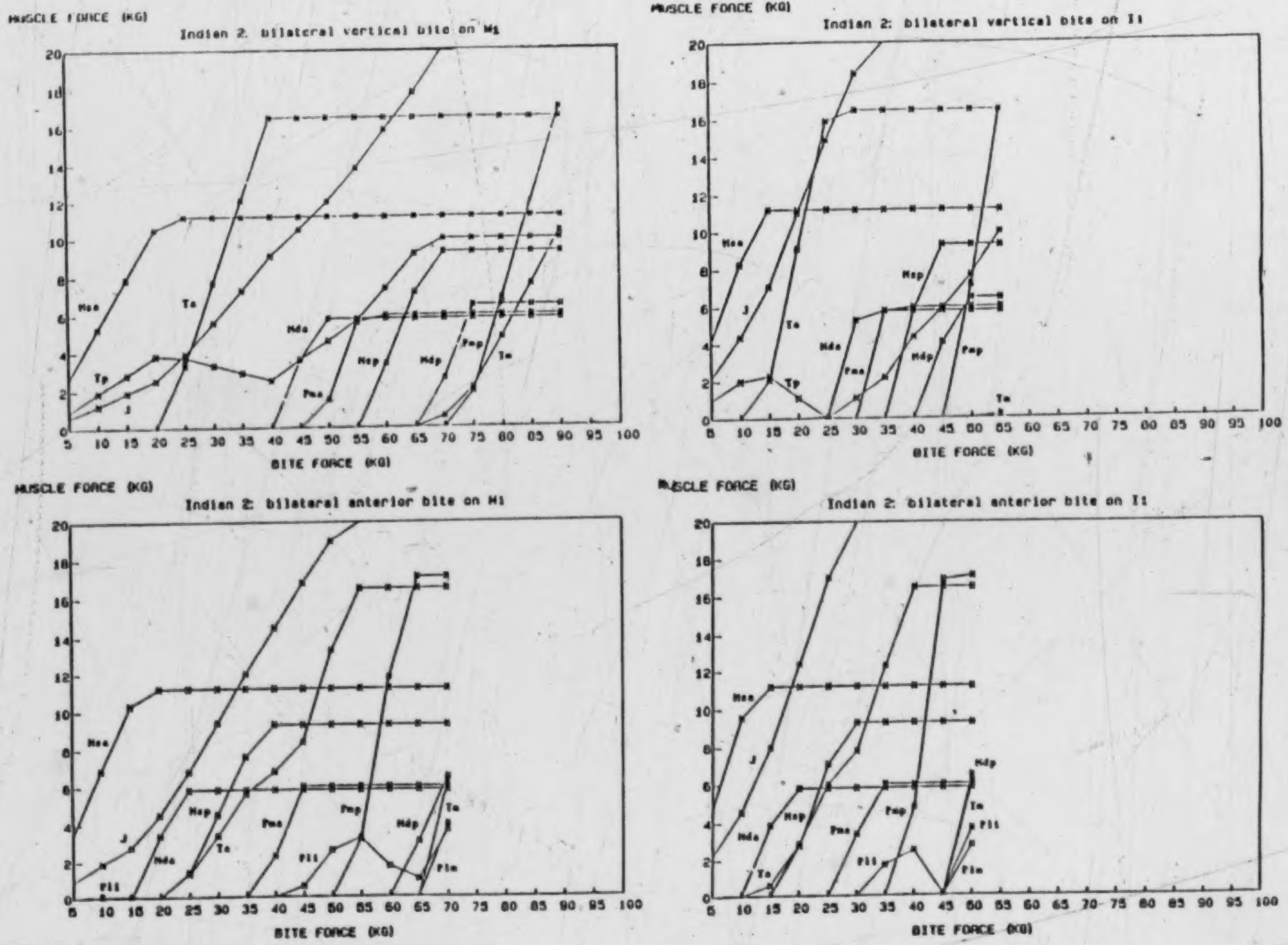


Fig. 42 Solutions for increasing bilateral bite forces for Indian 1 (I1).



Indian 2: bilateral vertical bite on M1

Indian 2: bilateral vertical bite on I1

Indian 2: bilateral anterior bite on M1

Indian 2: bilateral anterior bite on I1

Fig. 43 Solutions for increasing bilateral bite forces for Indian 2 (I2).

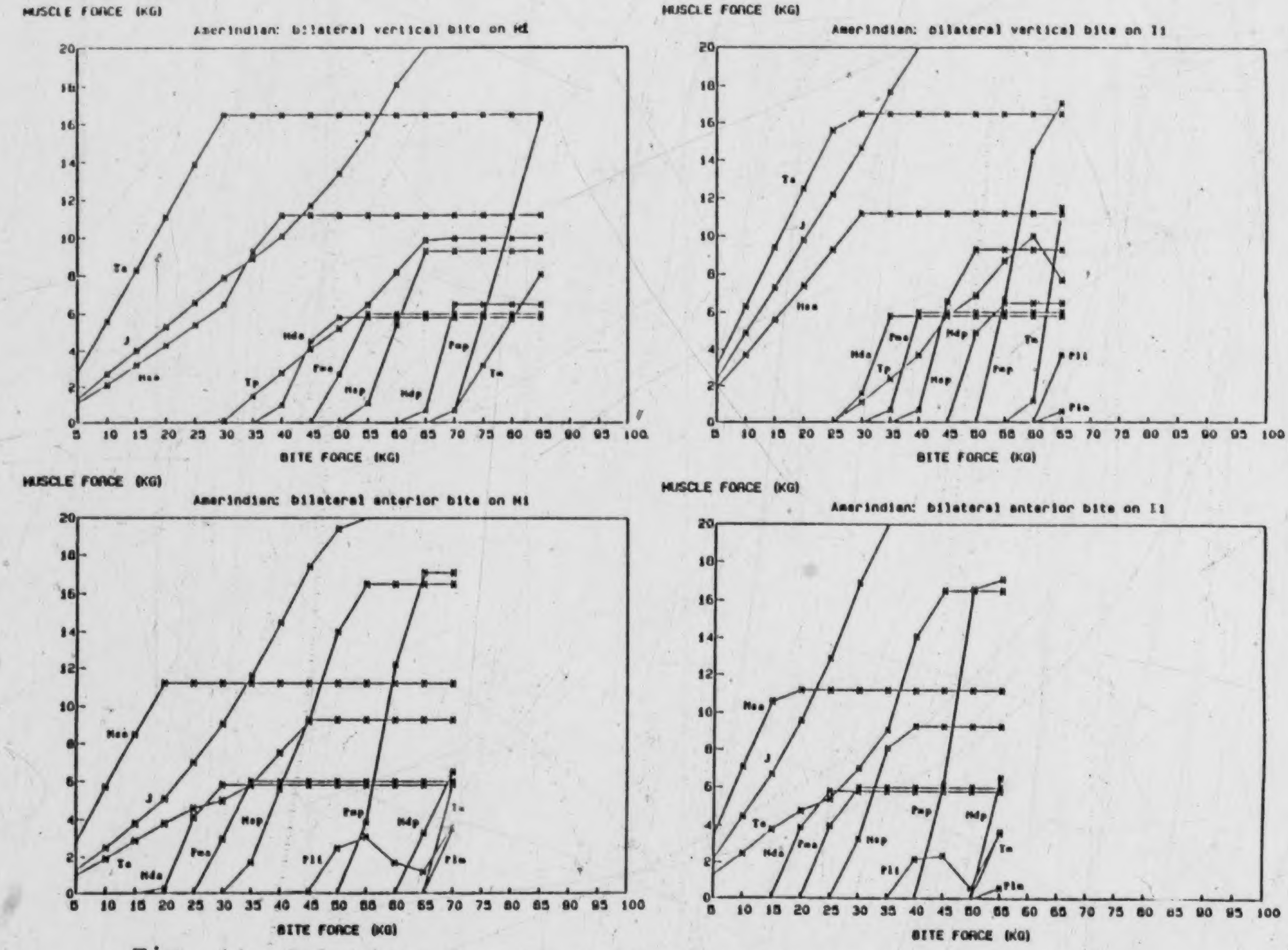
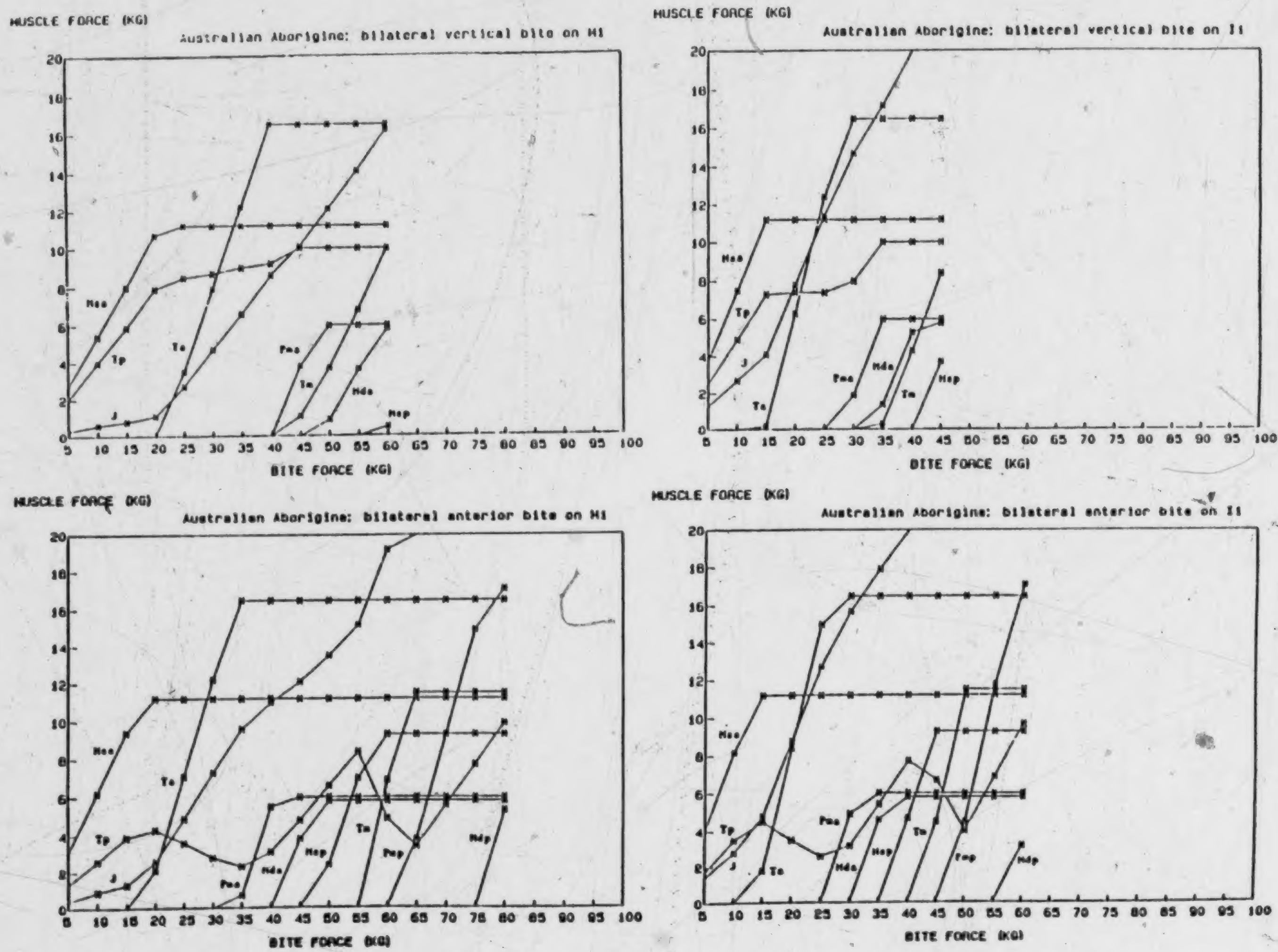


Fig. 44 Solutions for increasing bilateral bite forces for the Amerindian (AI).



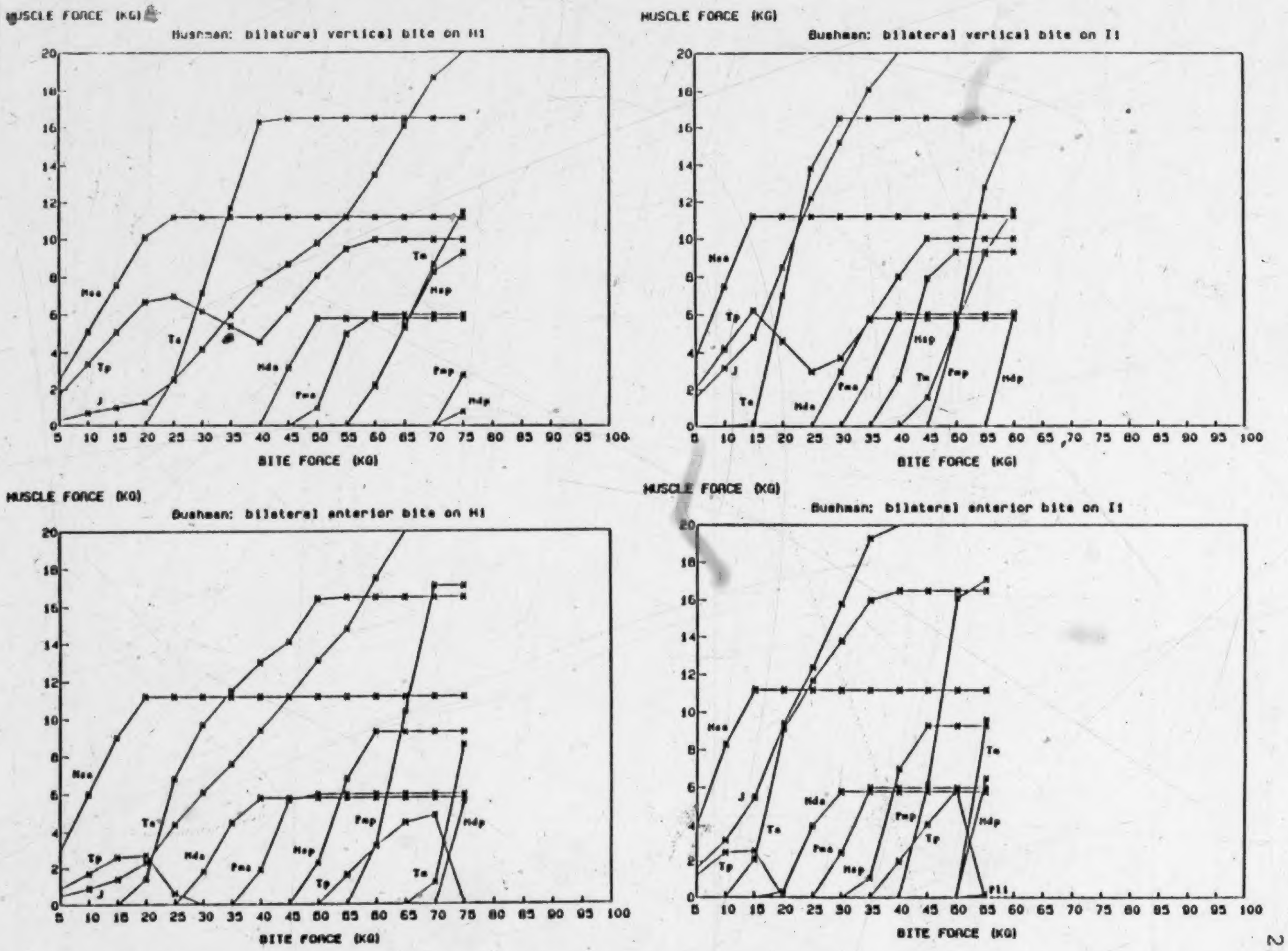
Australian Aborigine: bilateral vertical bite on M1

Australian Aborigine: bilateral vertical bite on I1

Australian Aborigine: bilateral anterior bite on M1

Australian Aborigine: bilateral anterior bite on I1

Fig. 45 Solutions for increasing bilateral bite forces for the Australian Aborigine (AA).



Bushman: bilateral vertical bite on M1

Bushman: bilateral vertical bite on I1

Bushman: bilateral anterior bite on M1

Bushman: bilateral anterior bite on I1

Fig. 46 Solutions for increasing bilateral bite forces for the Bushman (BM).

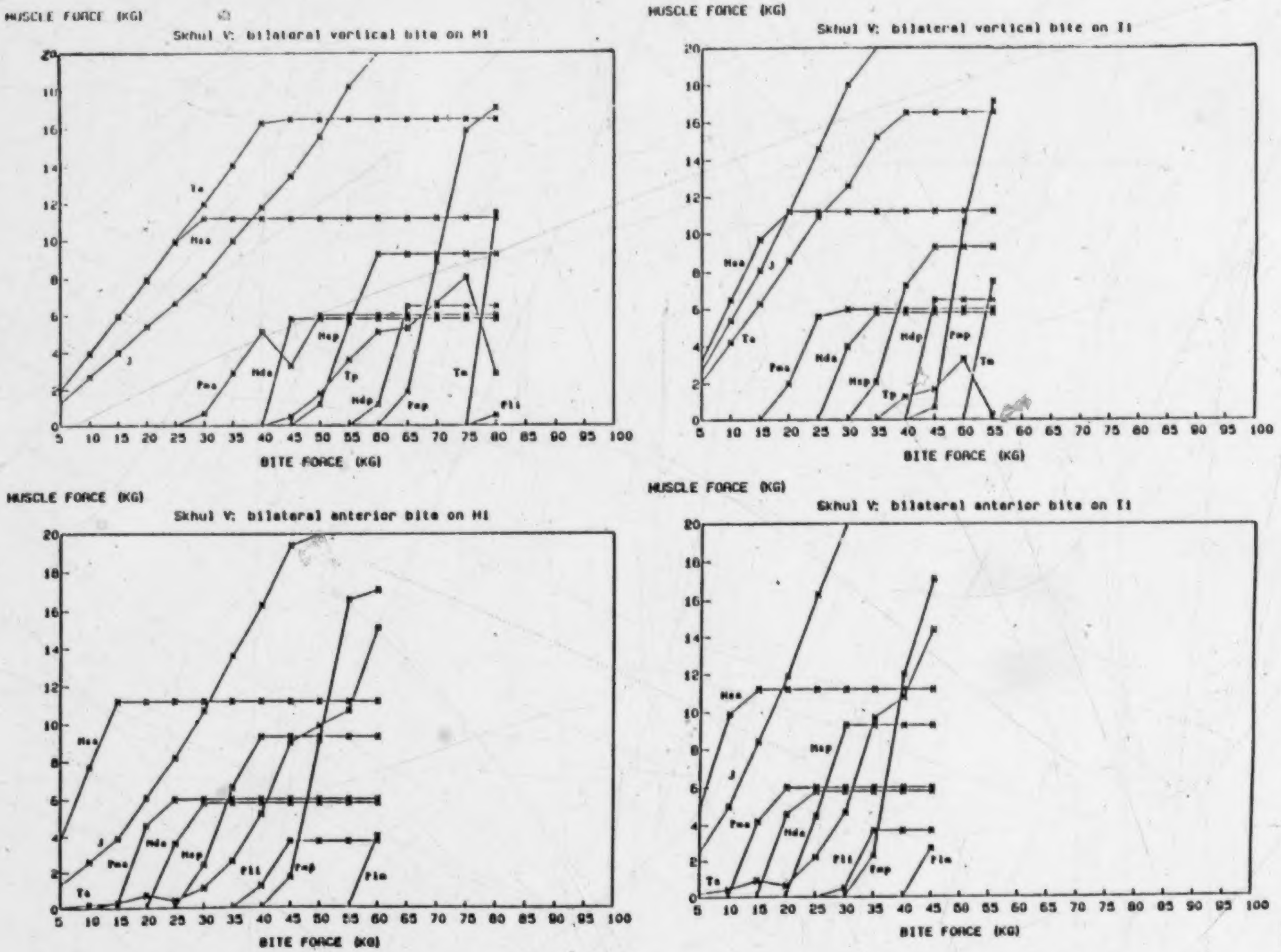


Fig. 47 Solutions for increasing bilateral bite forces for the Skhul V Hominid (SV).

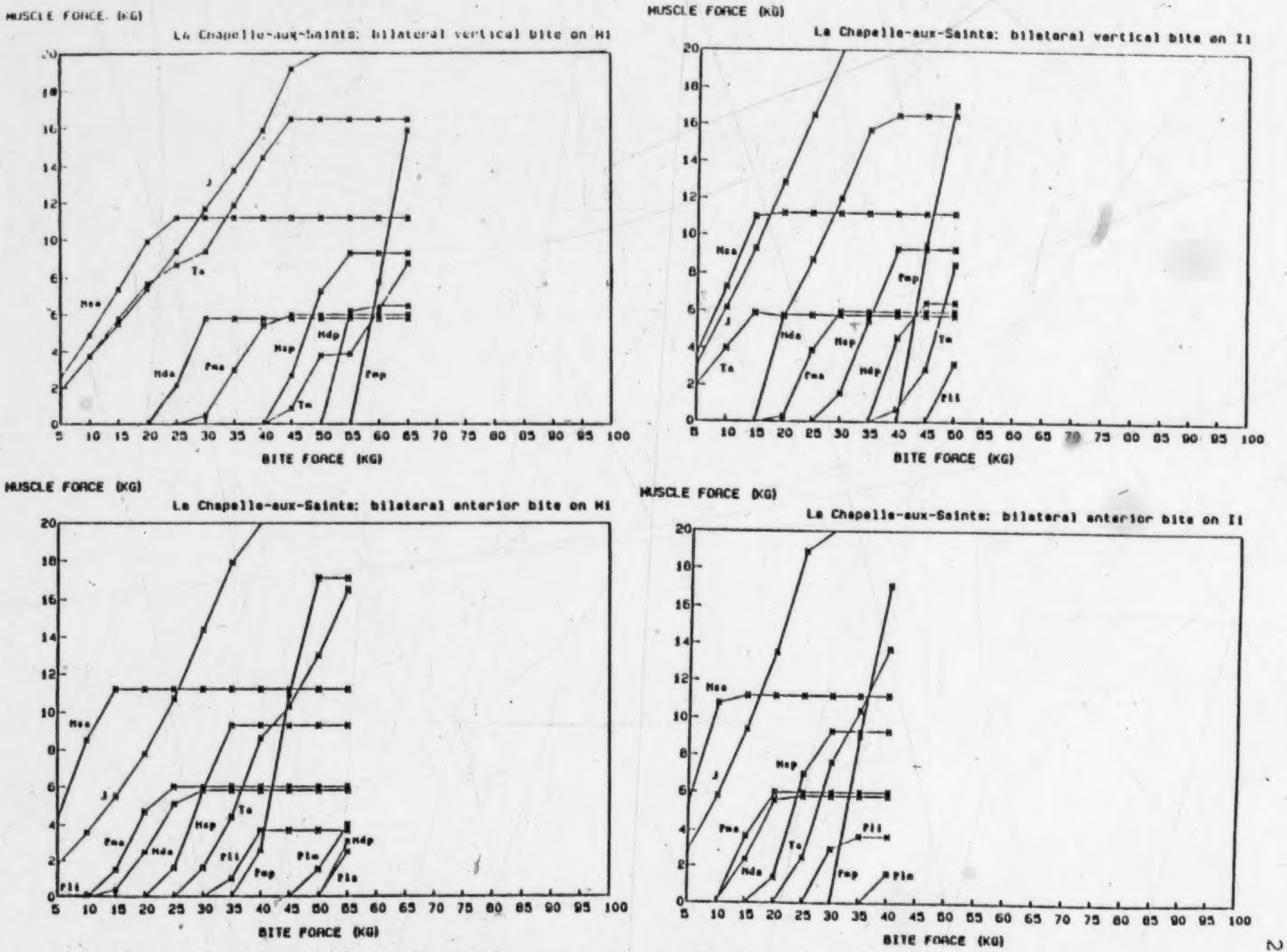


Fig. 48 Solutions for increasing bilateral bite forces for the La Chapelle-aux-Saints Hominid (CS).

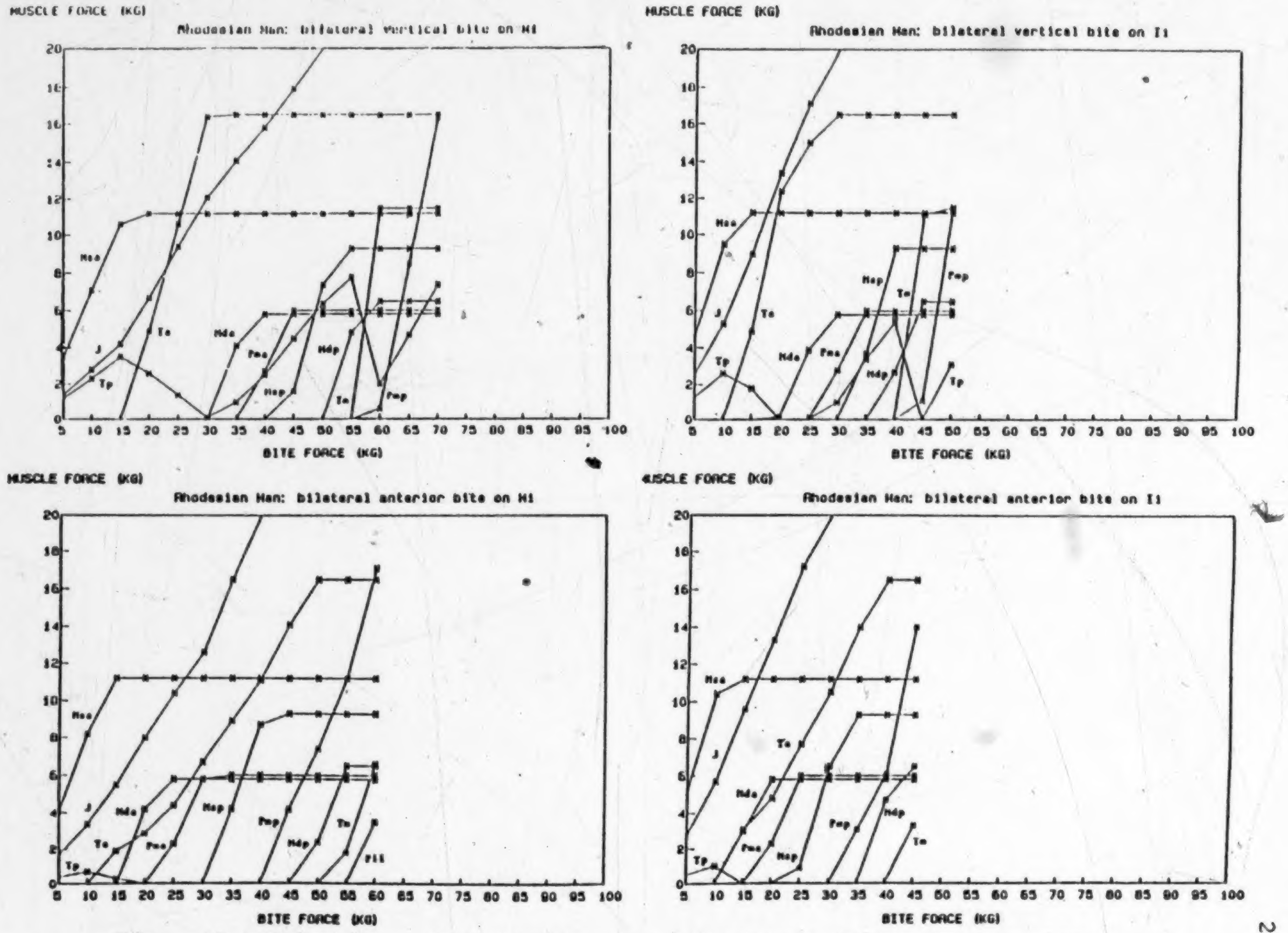


Fig. 49 Solutions for increasing bilateral bite forces for Rhodesian Man (RM).

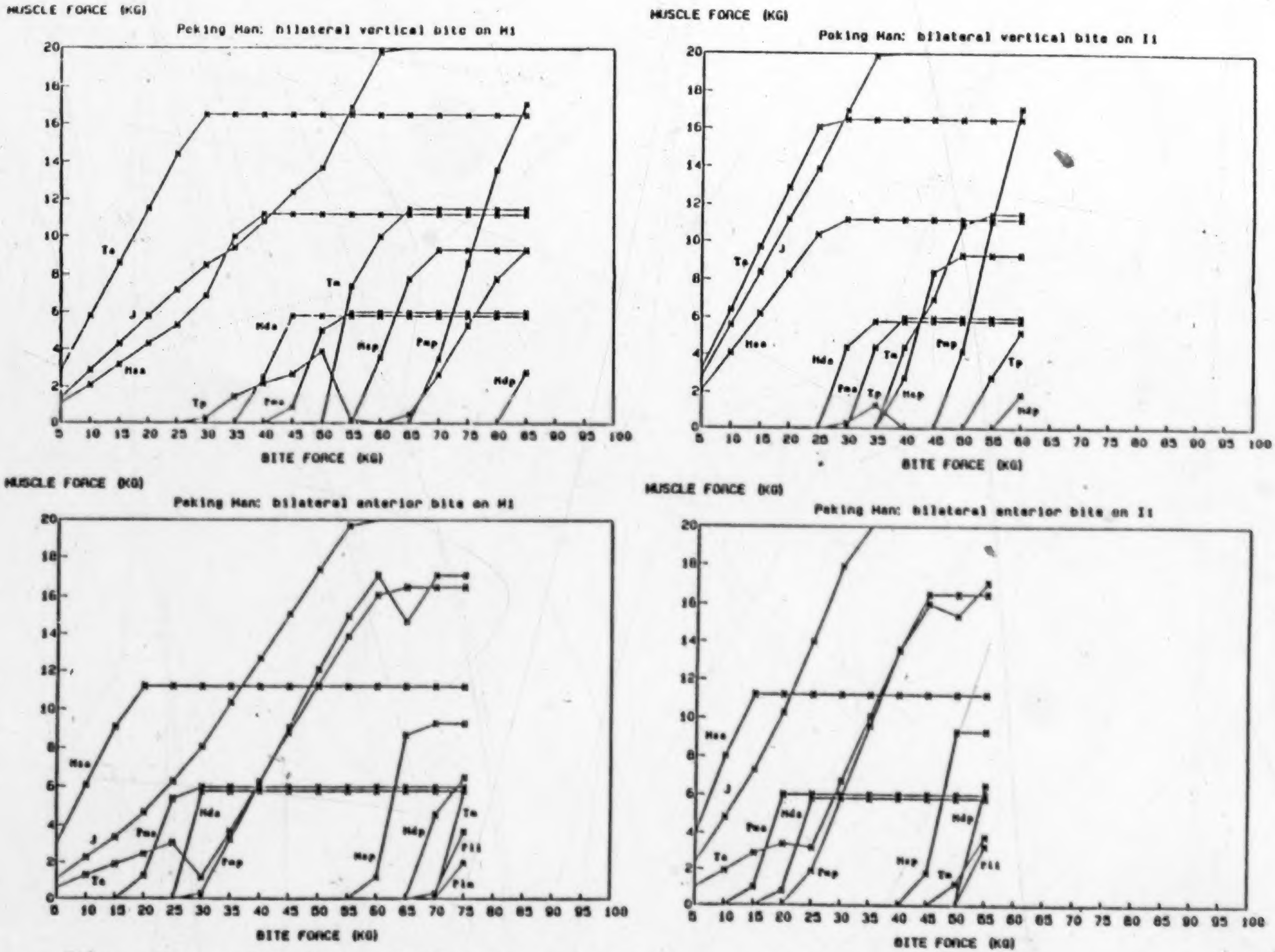


Fig. 50 Solutions for increasing bilateral bite forces for Peking Man (PM).

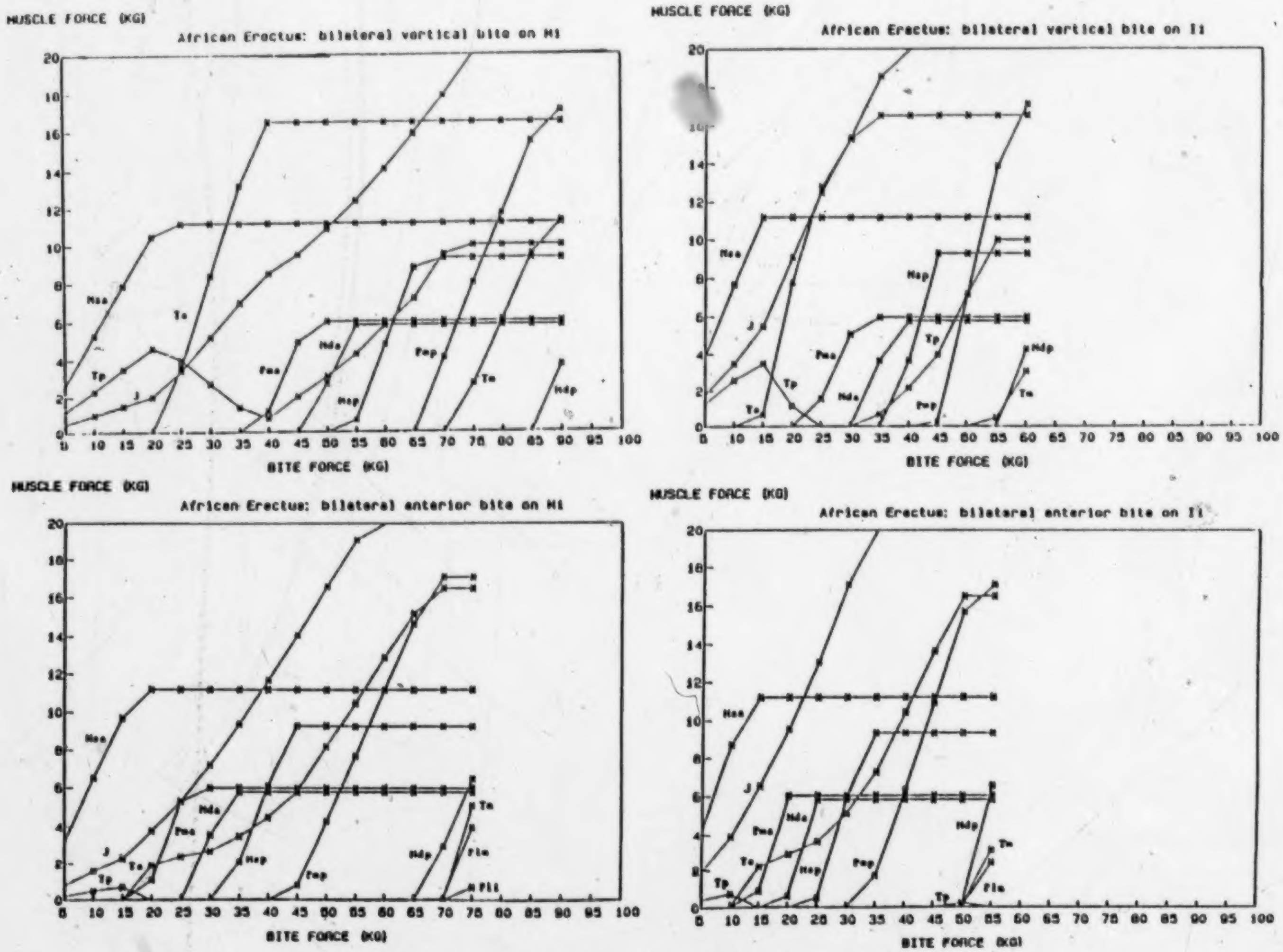


Fig. 51 Solutions for increasing bilateral bite forces for the African Erectus (AE).

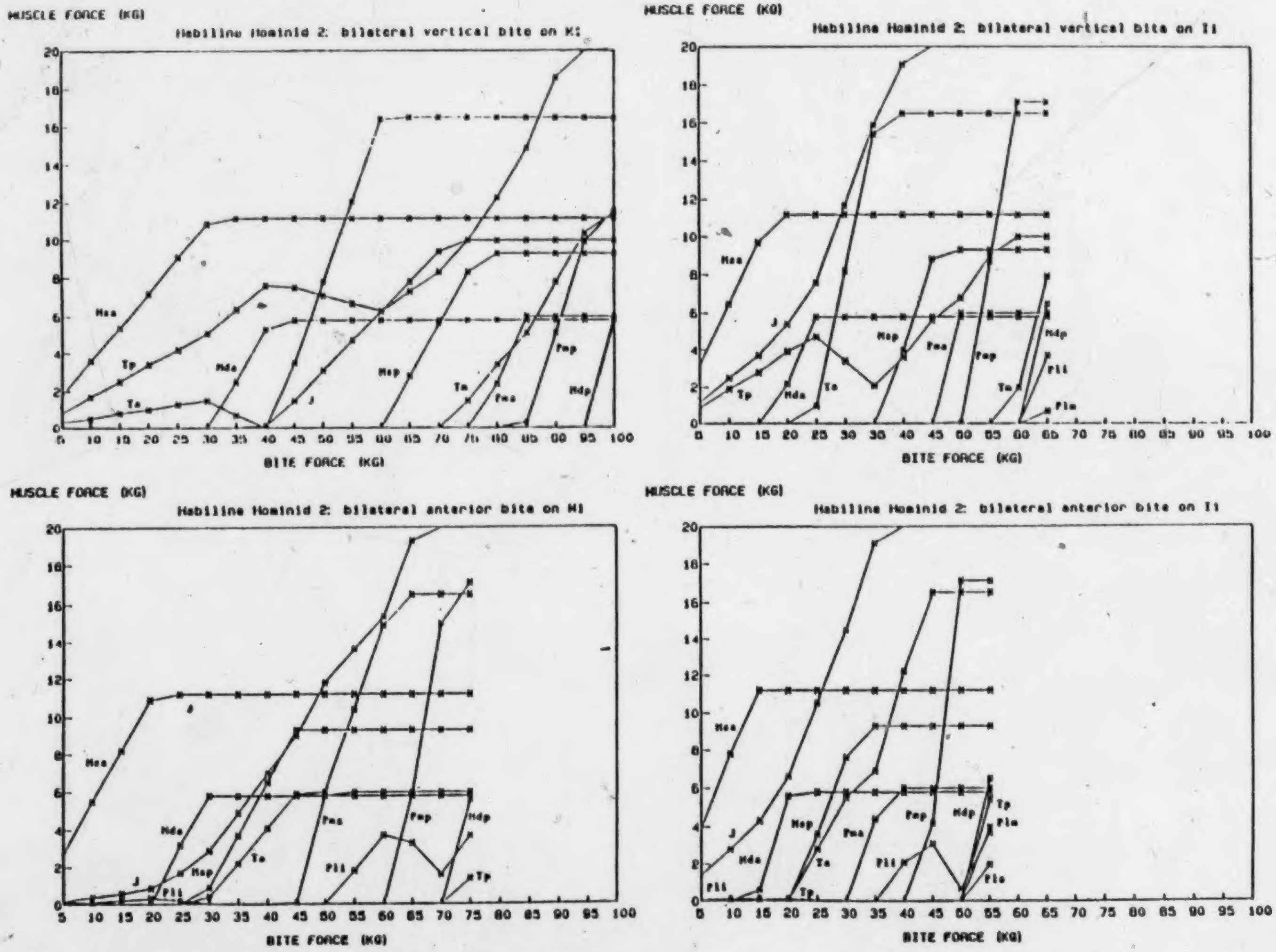


Fig. 52 Solutions for increasing bilateral bite forces for Habiline Hominid 2 (H2).

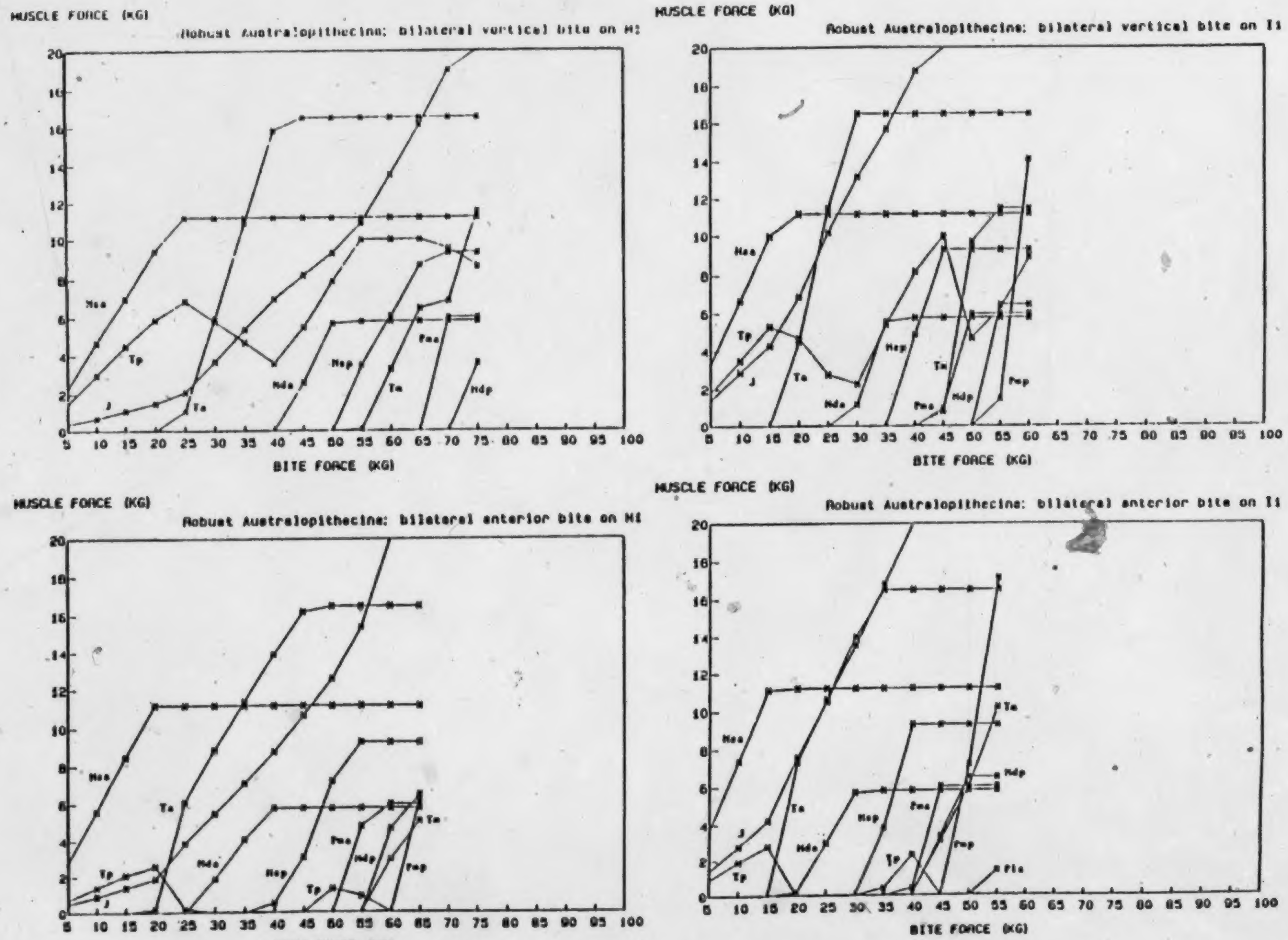


Fig. 53 Solutions for increasing bilateral bite forces for the Robust Australopithecine (RA).

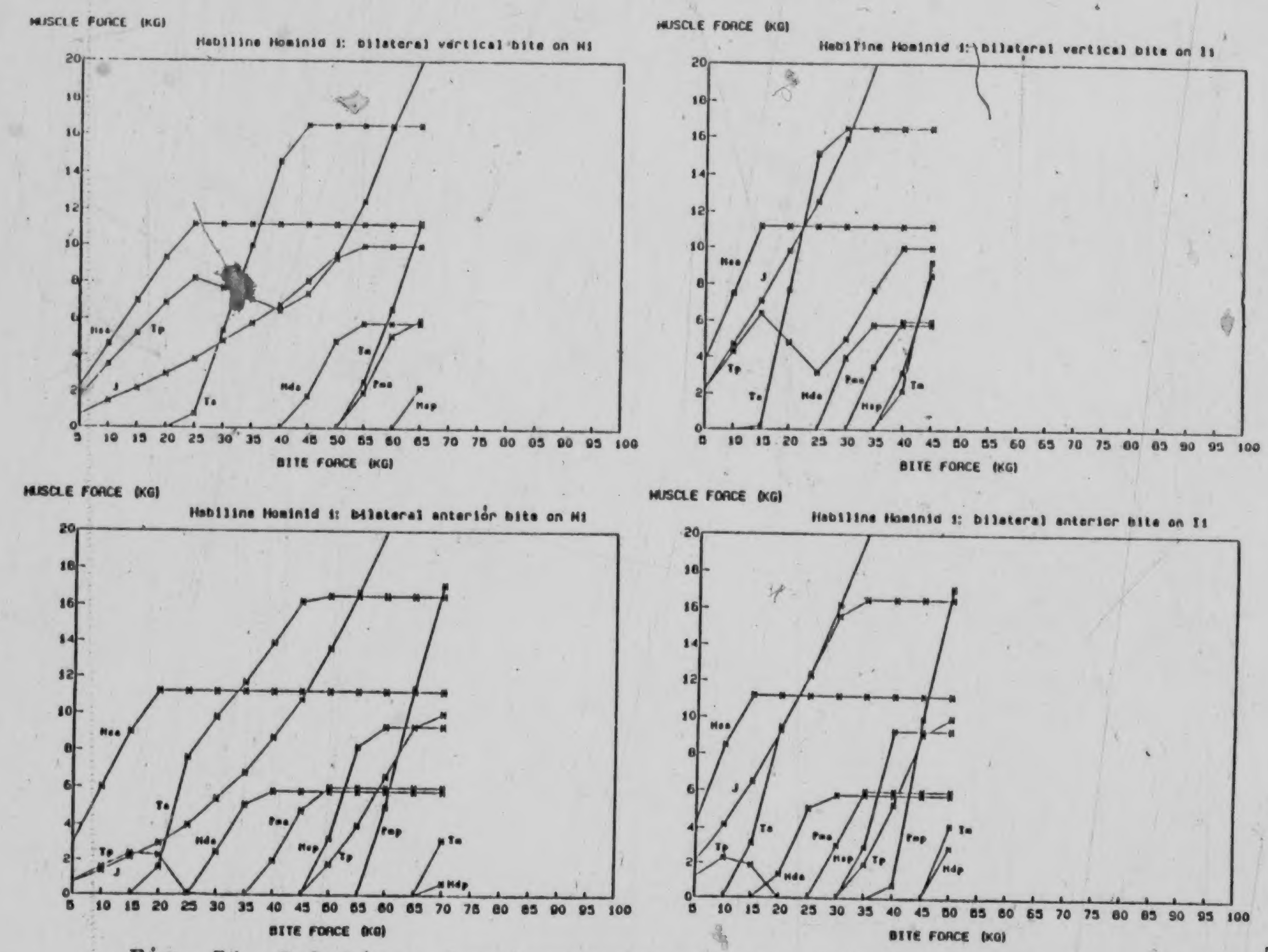


Fig. 54 Solutions for increasing bilateral bite forces for Habiline Hominid 1 (H1).

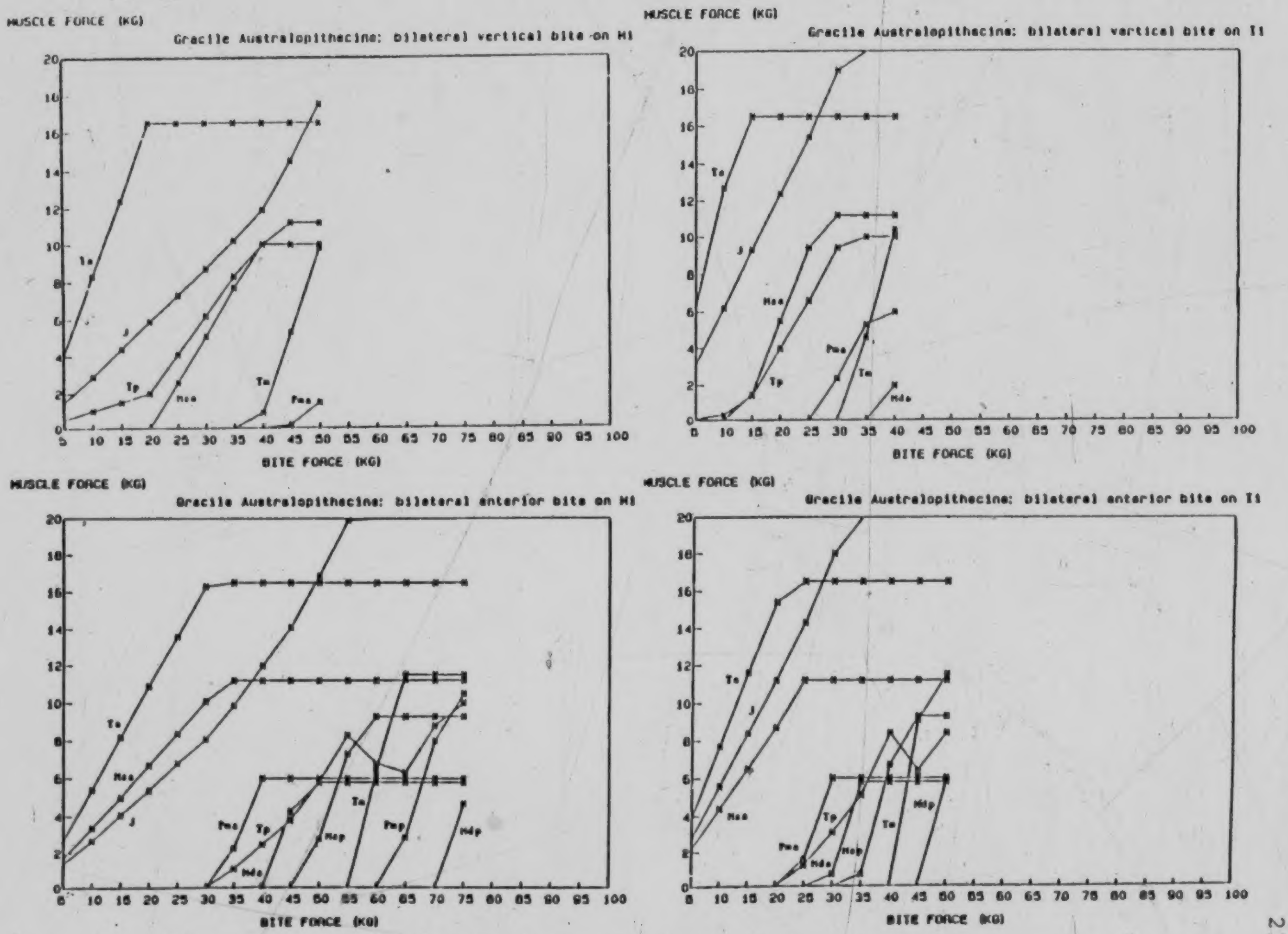


Fig. 55 Solutions for increasing bilateral bite forces for the Gracile Australopithecine (GA).

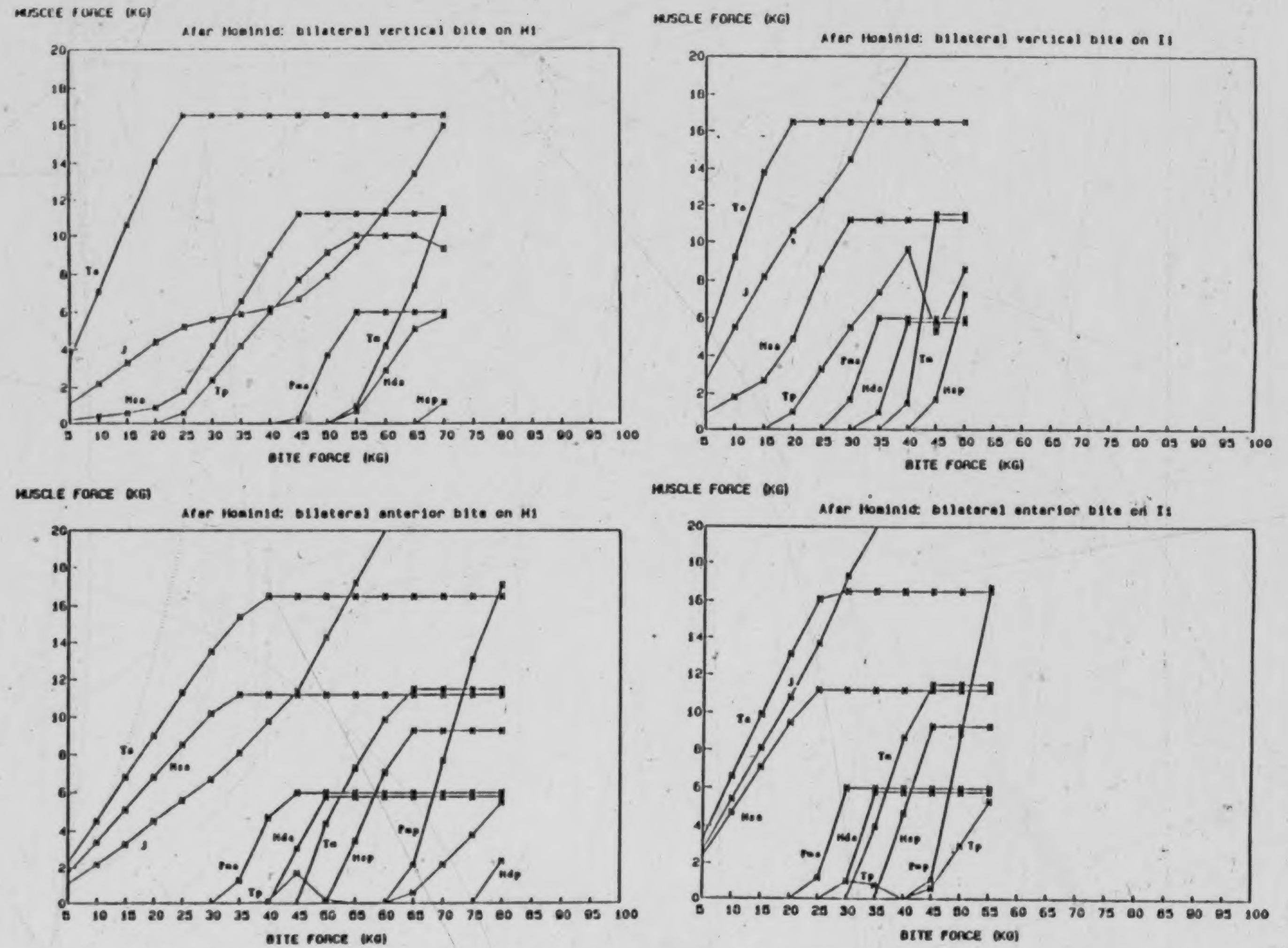


Fig. 56 Solutions for increasing bilateral bite forces for the Afar Hominid (AH).

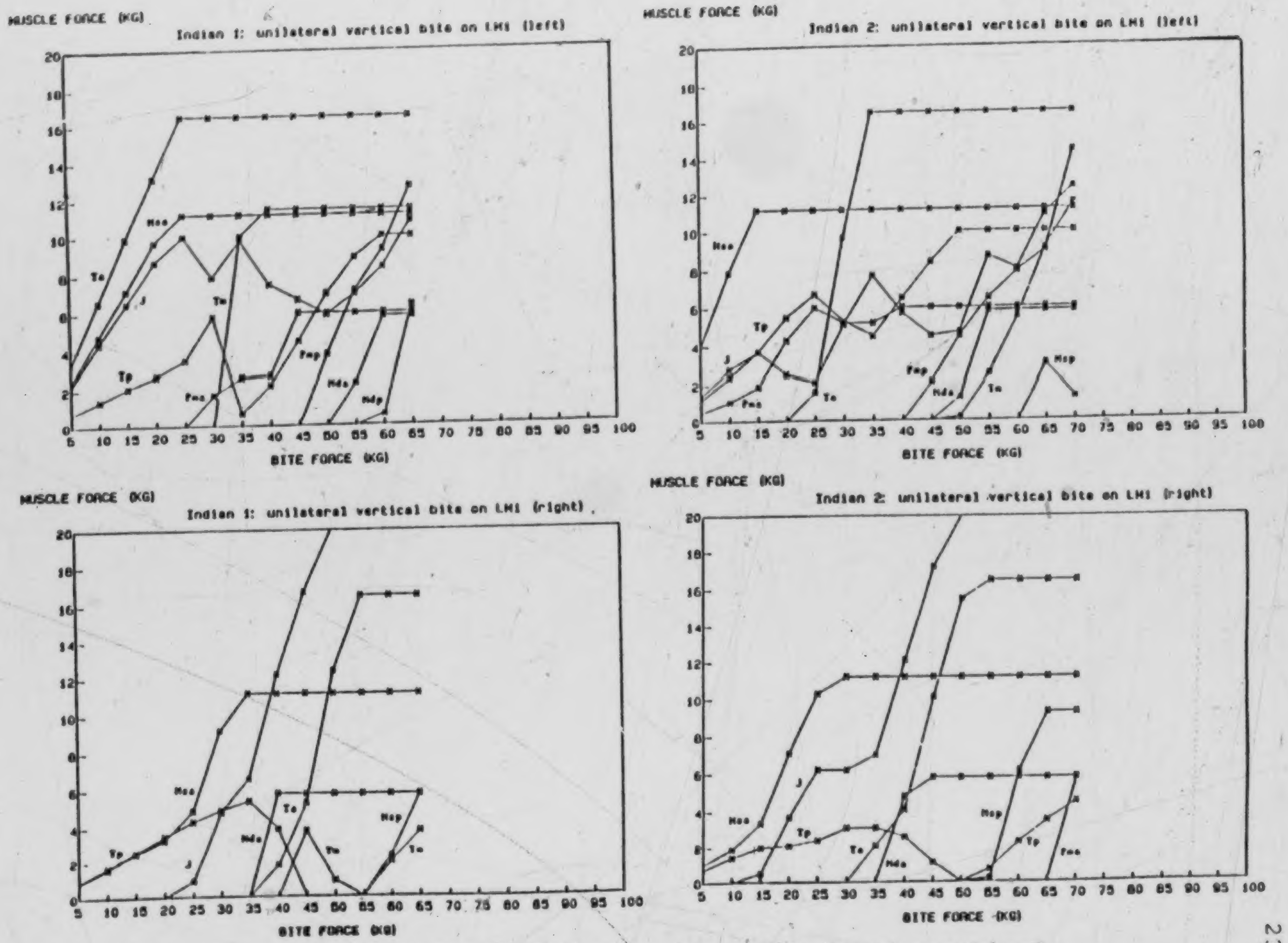


Fig. 57 Solutions for an increasing unilateral vertical molar bite force for the w.s. (above) and the b.s. (below) for Indian 1 (left) and Indian 2 (right).

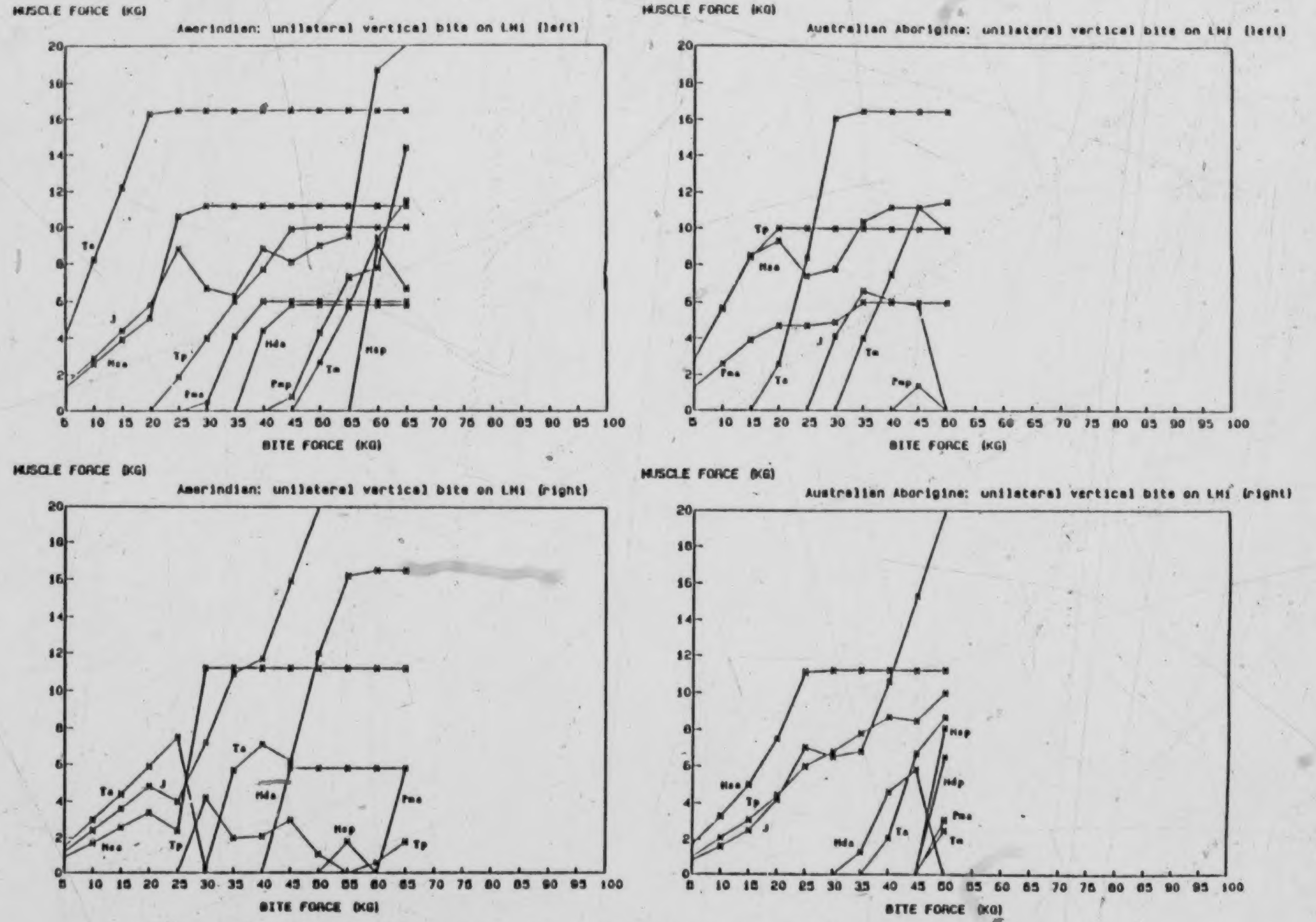


Fig. 58 Solutions for an increasing unilateral vertical molar bite force for the w.s. (above) and the b.s. (below) for the Amerindian (left) and the Australian Aborigine (right).

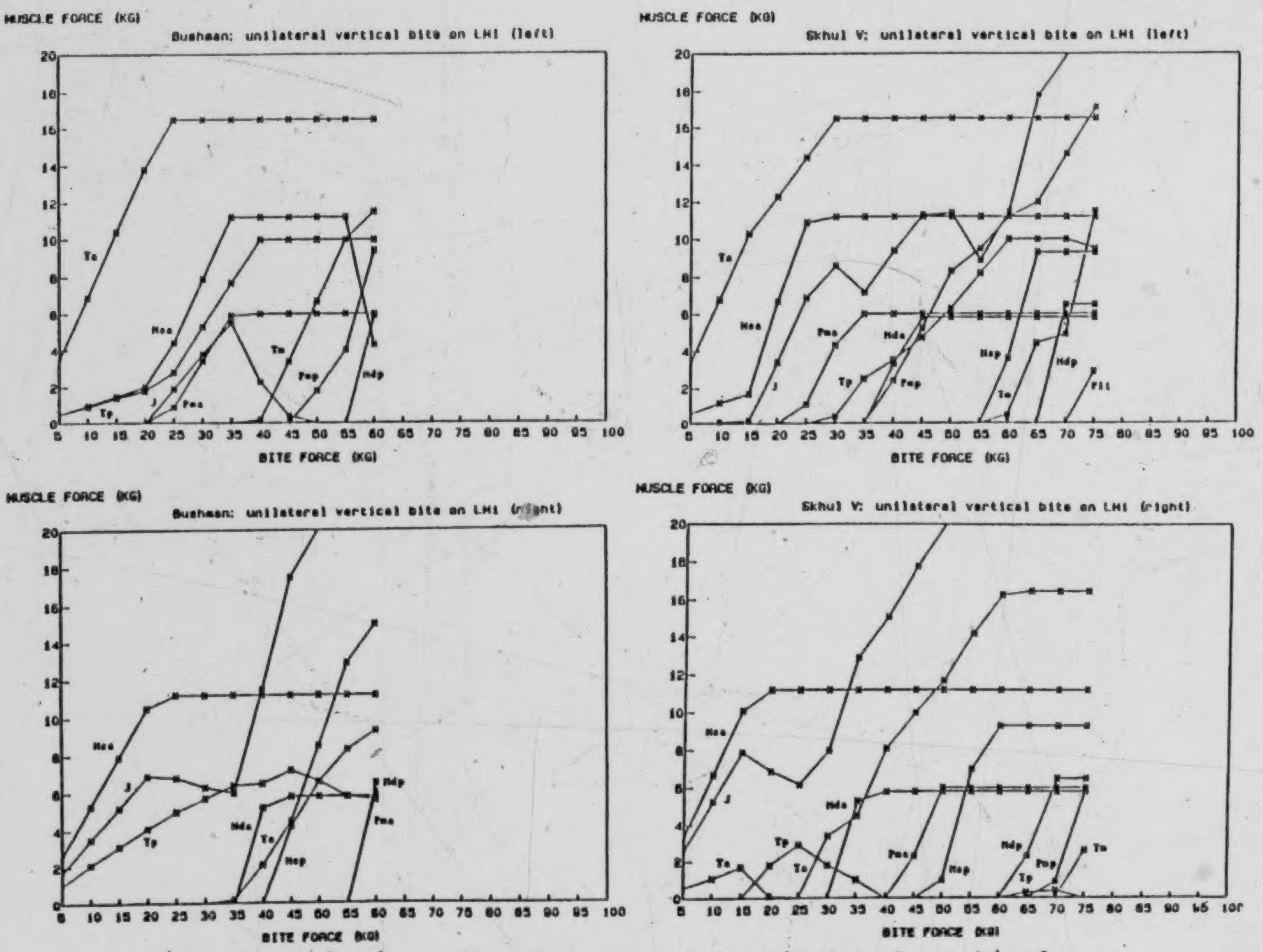


Fig. 59 Solutions for an increasing unilateral vertical molar bite force for the w.s. (above) and the b.s. (below) for the Bushman (left) and the Skhul V Hominid (right).

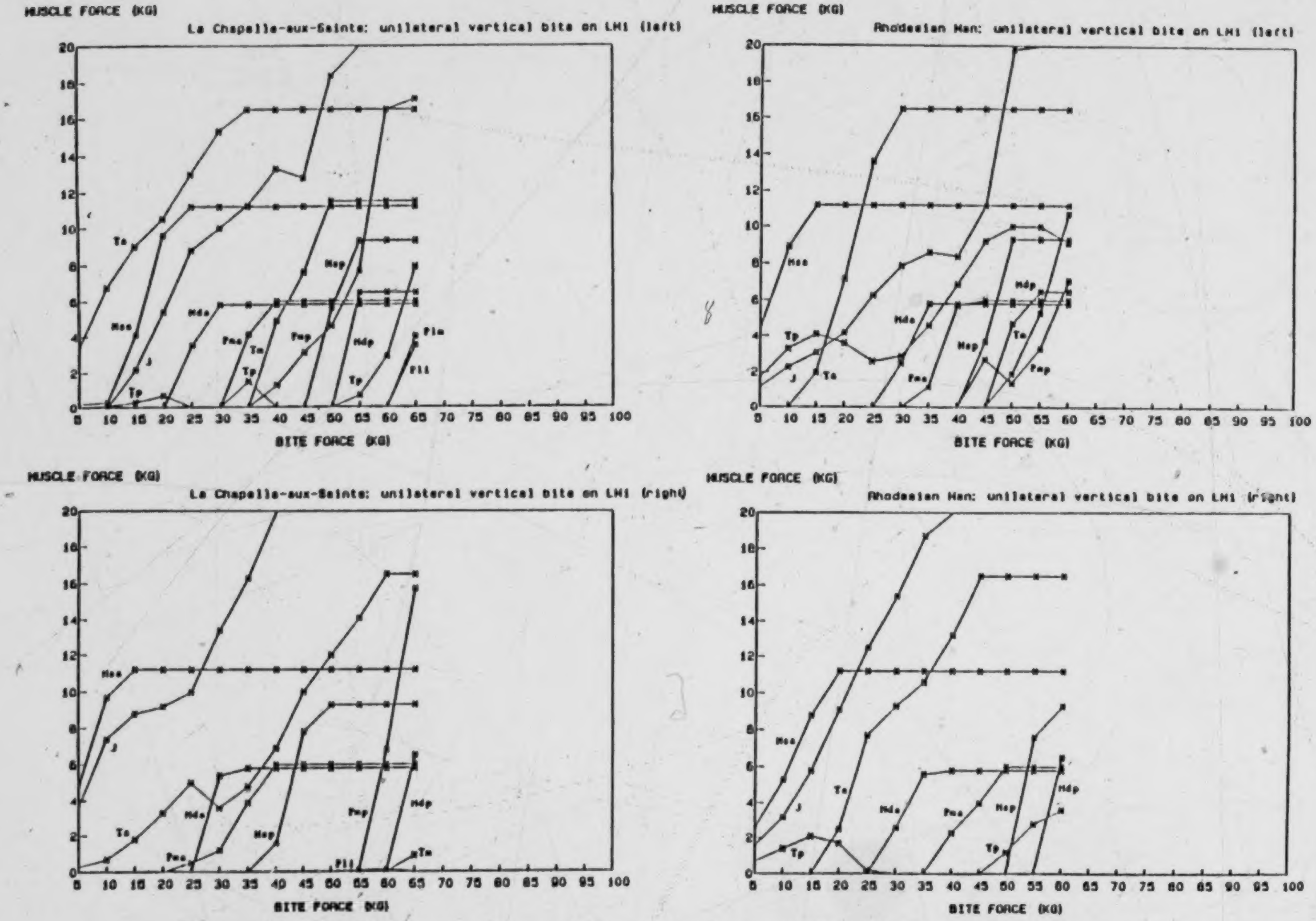


Fig. 60 Solutions for an increasing unilateral vertical molar bite force for the w.s. (above) and the b.s. (below) for the La Chapelle-aux-Saints Hominid (left) and Rhodesian Man (right).

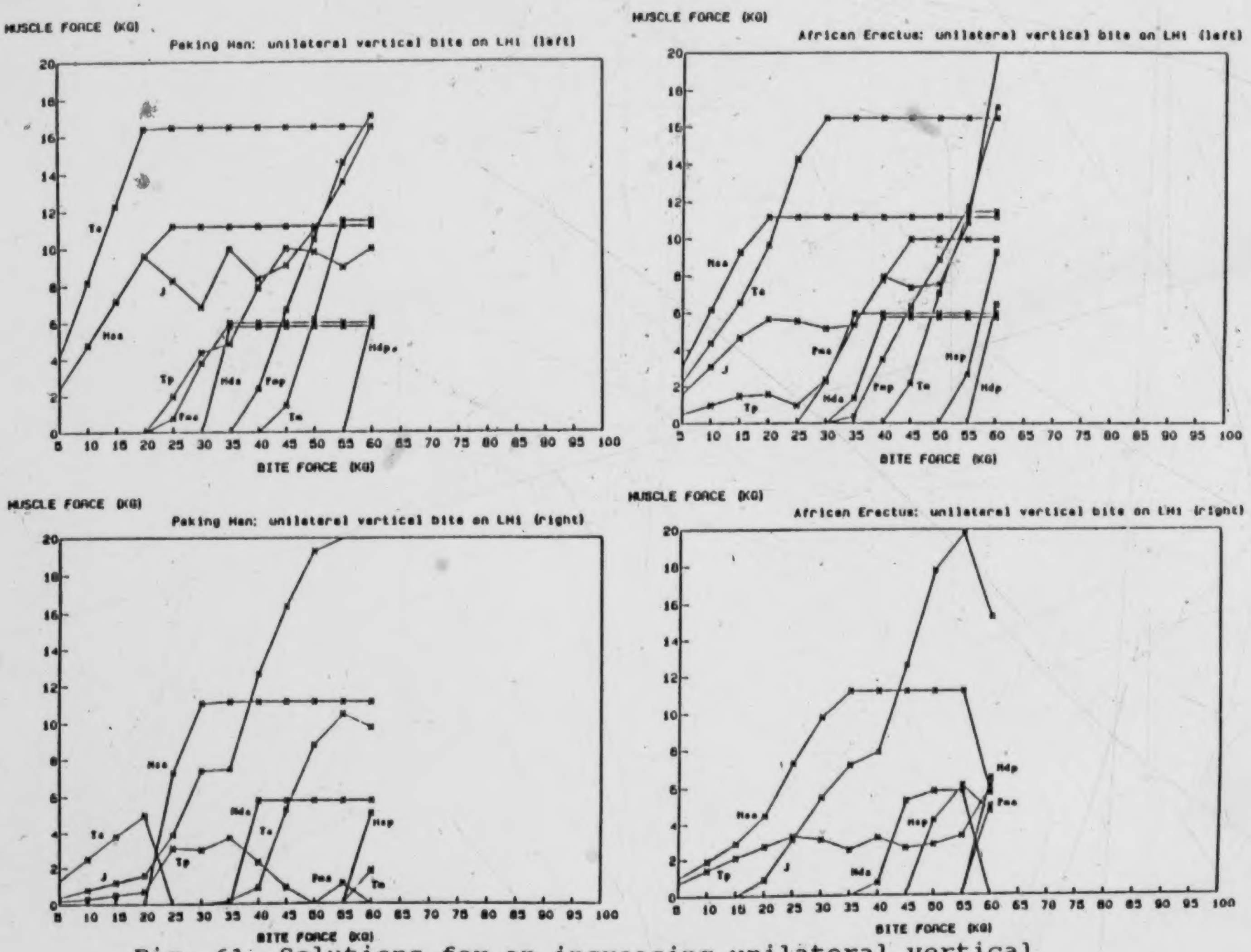


Fig. 61 Solutions for an increasing unilateral vertical molar bite force for the w.s. (above) and the b.s. (below) for Peking Man (left) and the African Erectus (right).

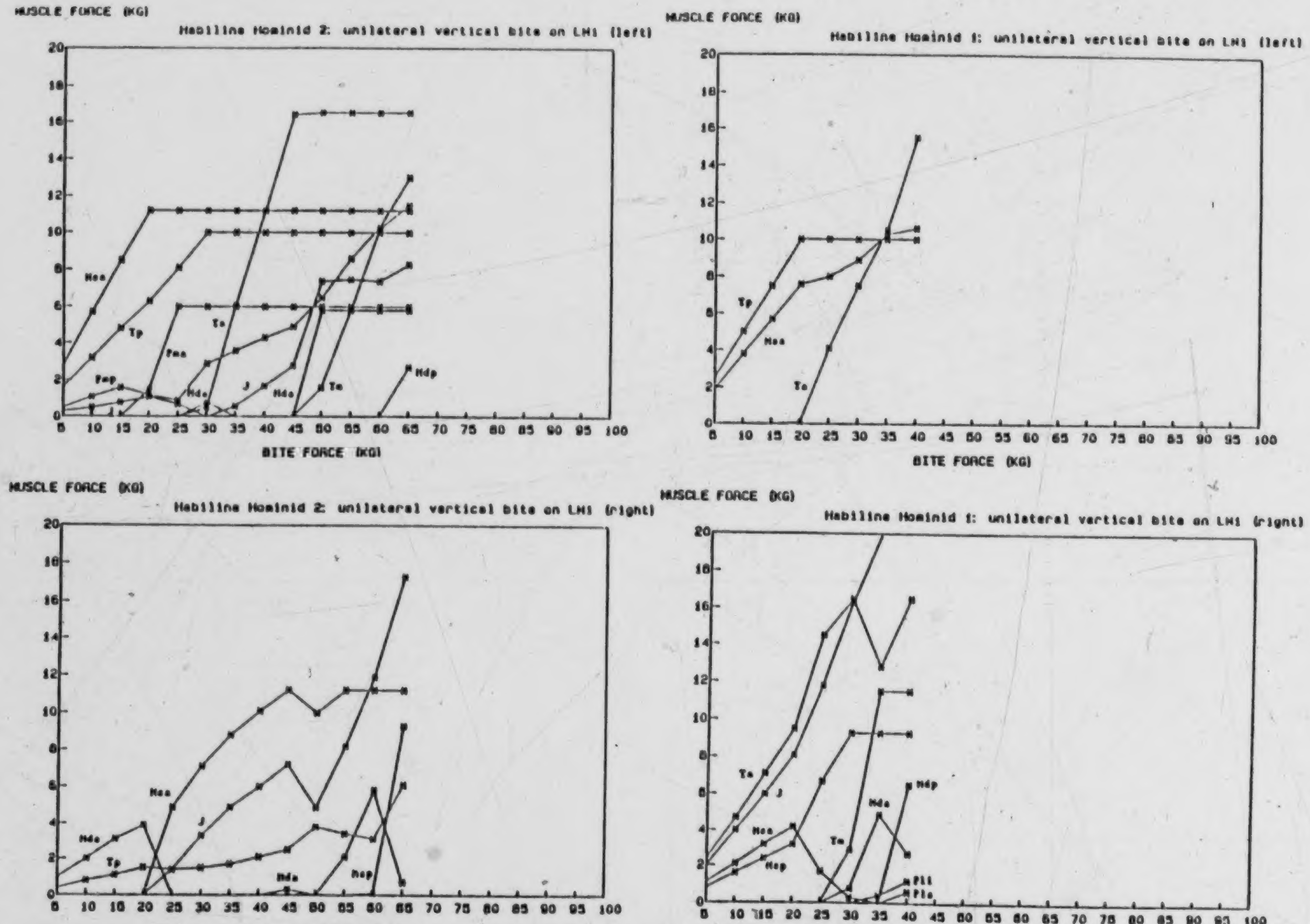


Fig. 62 Solutions for an increasing unilateral vertical molar bite force for the w.s. (above) and the b.s. (below) for Habiline Hominid 2 (left) and Habiline Hominid 1 (right).

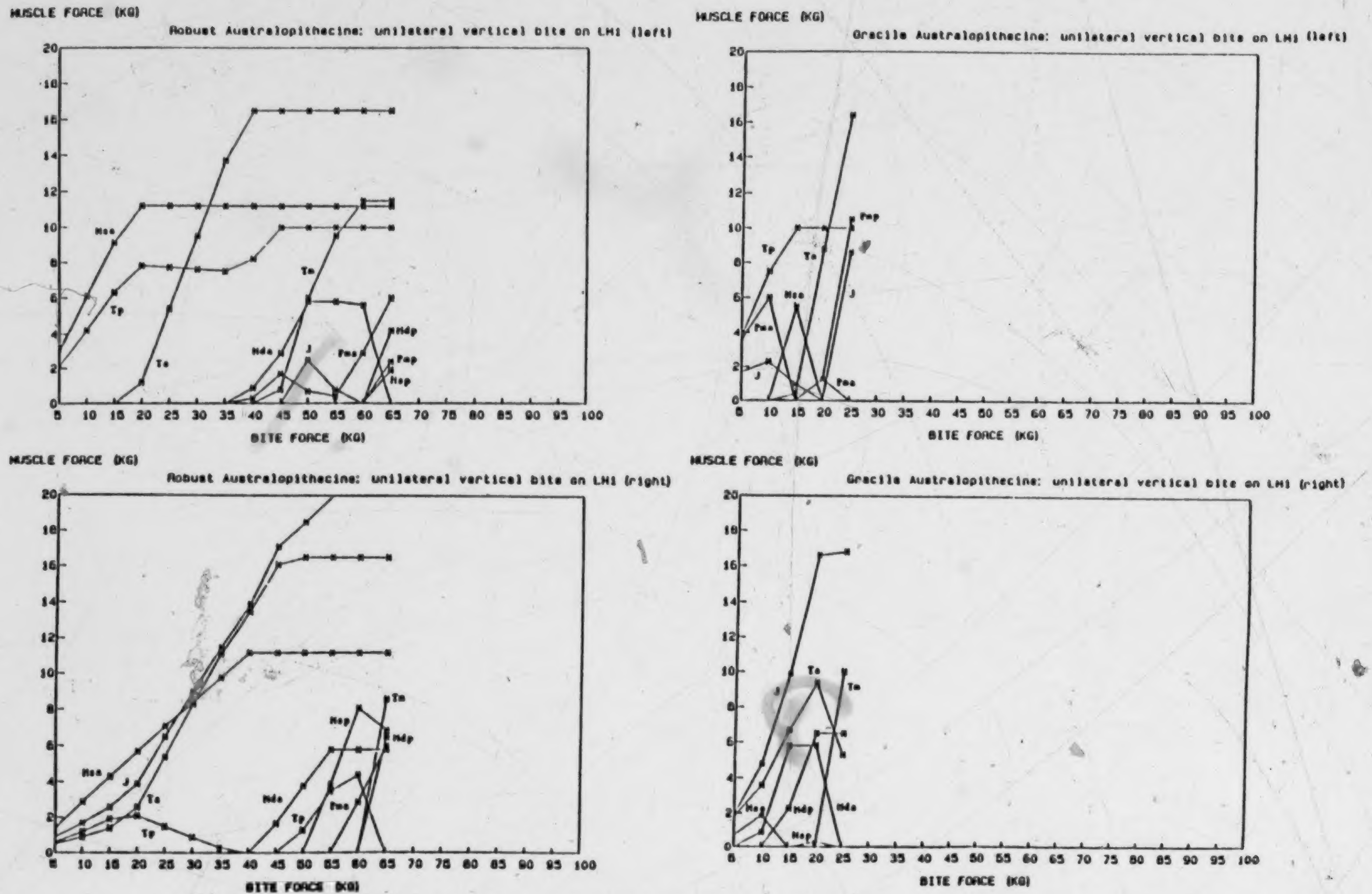


Fig. 63 Solutions for an increasing unilateral vertical molar bite force for the w.s. (above) and the b.s. (below) for the Robust Australopithecine (left) and the Gracile Australopithecine (right).

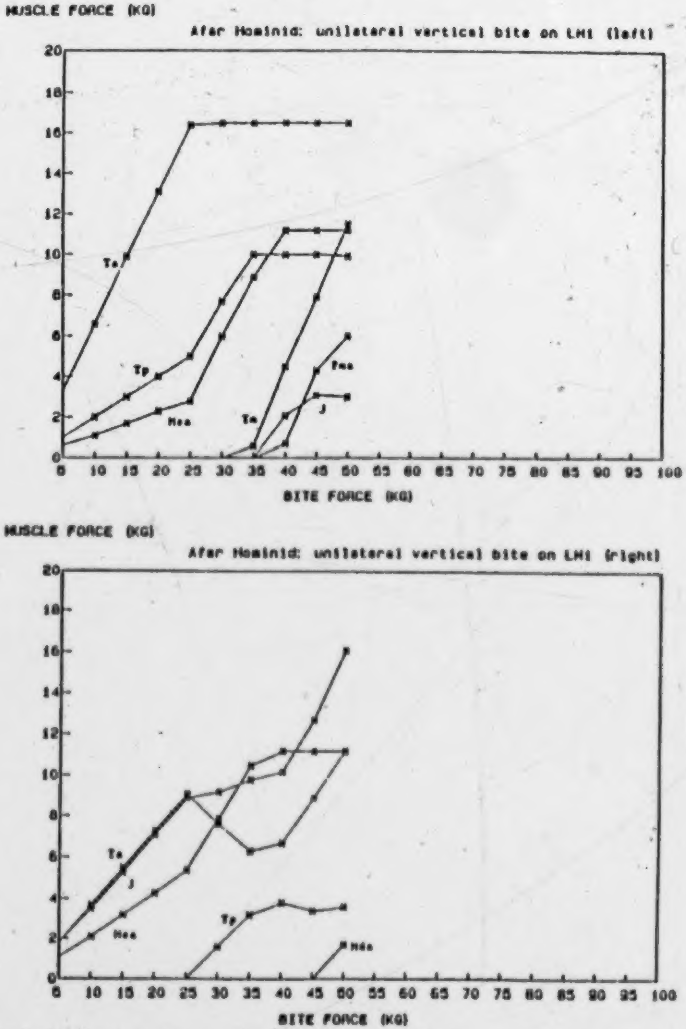
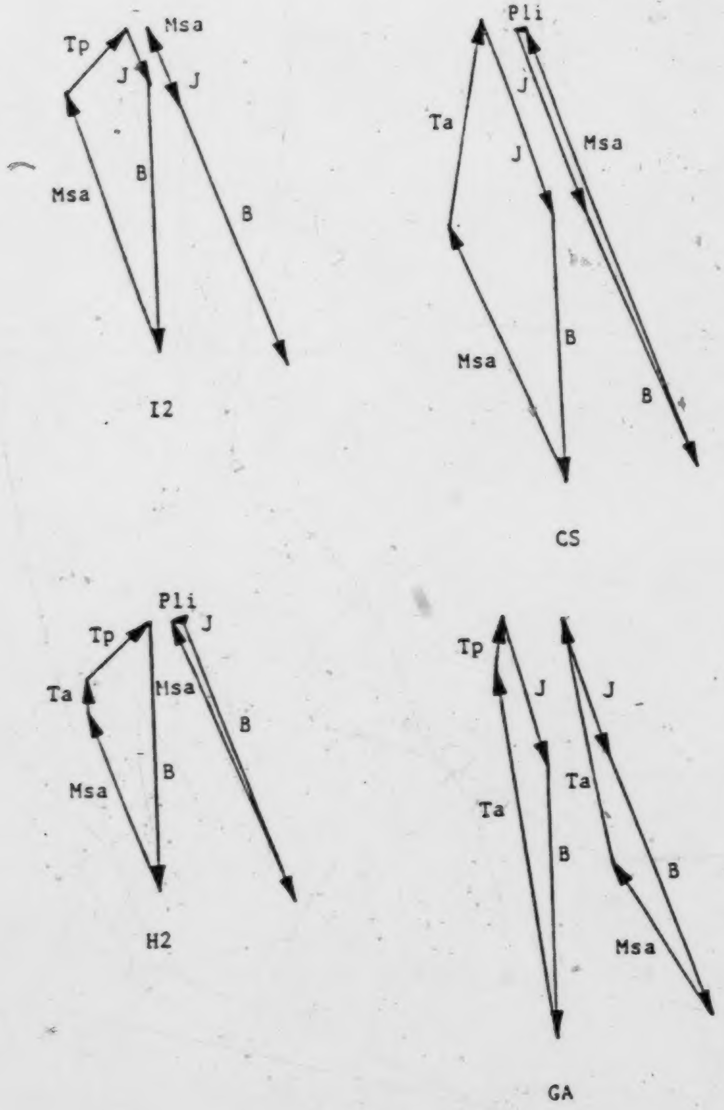


Fig. 64 Solutions for an increasing unilateral vertical molar bite force for the w.s. (above) and the b.s. (below) for the Afar Hominid.


Tp
Msa
J
J
Msa
B
B
Pli
Ta
J
J
Msa
Msa
B
B
Pli
Tp
J
Ta
Msa
Msa
B
B
Tp
J
J
Ta
Ta
B
B
Msa

I2

CS

H2

GA

Fig. 65 Geometric equilibrium for the 5kg bilateral vertical and anterior (bold) molar bites for Indian 1 (I1), the La Chapelle-aux-Saints Hominid (CS), Habiline Hominid 2 (H2) and the Gracile Australopithecine (GA).

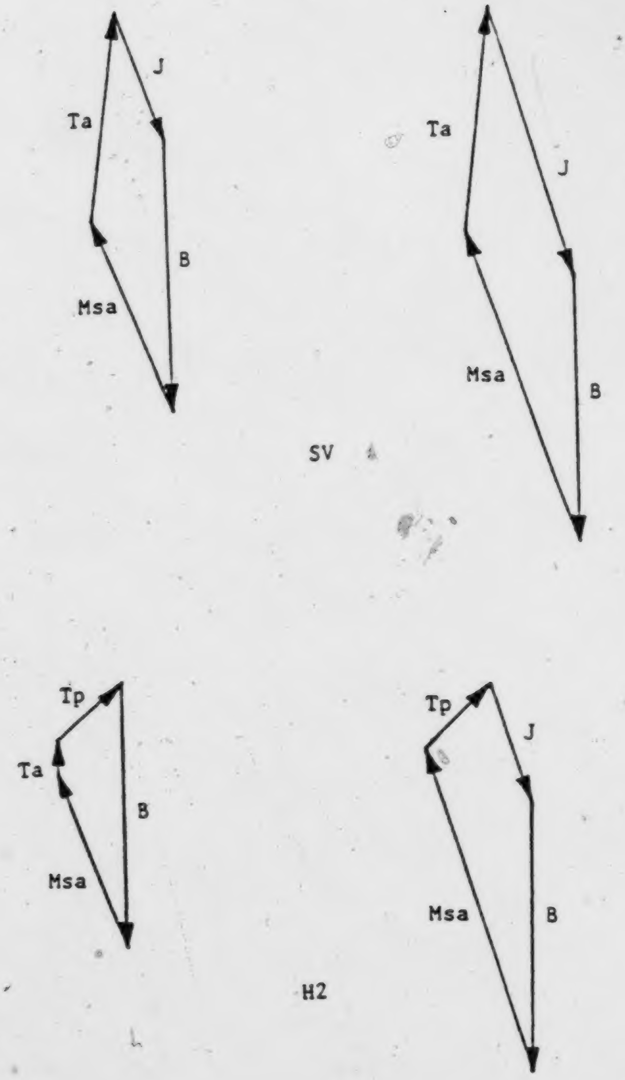

Ta
J
B
Msa
Ta
J
Msa
B
SV
Tp
Ta
B
Msa
Tp
J
Msa
B
H2

Fig. 66 Geometric equilibrium for the 5kg bilateral vertical molar (left) and incisor (right) bites for the Skhul V Hominid (SV) and Habiline Hominid 2 (H2).

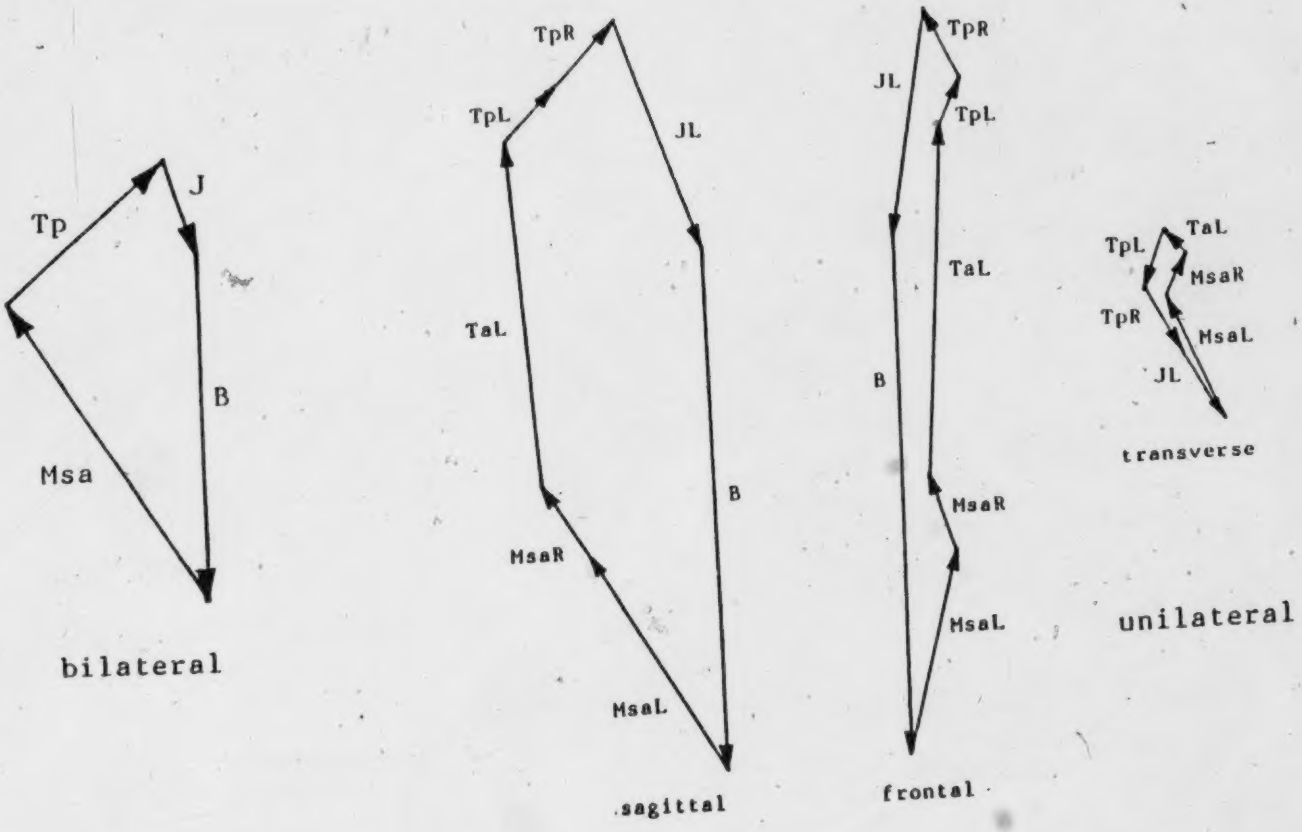

Tp
J
B
Msa
bilateral
TpR
TpL
JL
TaL
B
MsaR
MsaL
sagittal
TpR
JL
TpL
TaL
B
MsaR
MsaL
frontal
TpL
TaL
MsaR
TpR
MsaL
JL
transverse
unilateral

Fig. 67 Geometric equilibrium for the 5kg bilateral and unilateral vertical molar bites for Indian 1.

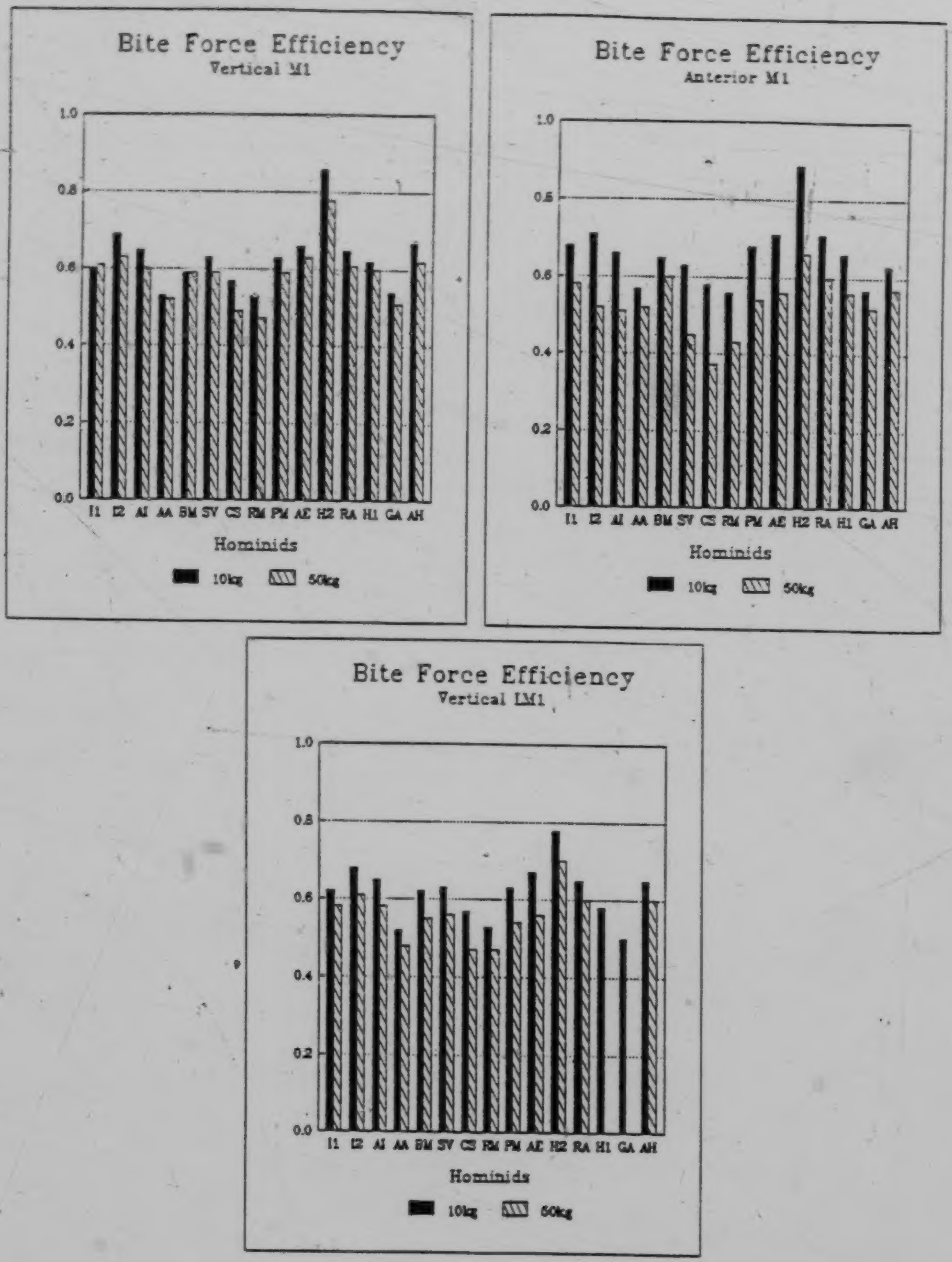


Fig. 68 Bite force efficiency of the hominids for selected molar bites (missing bars indicate no solution to the problem).

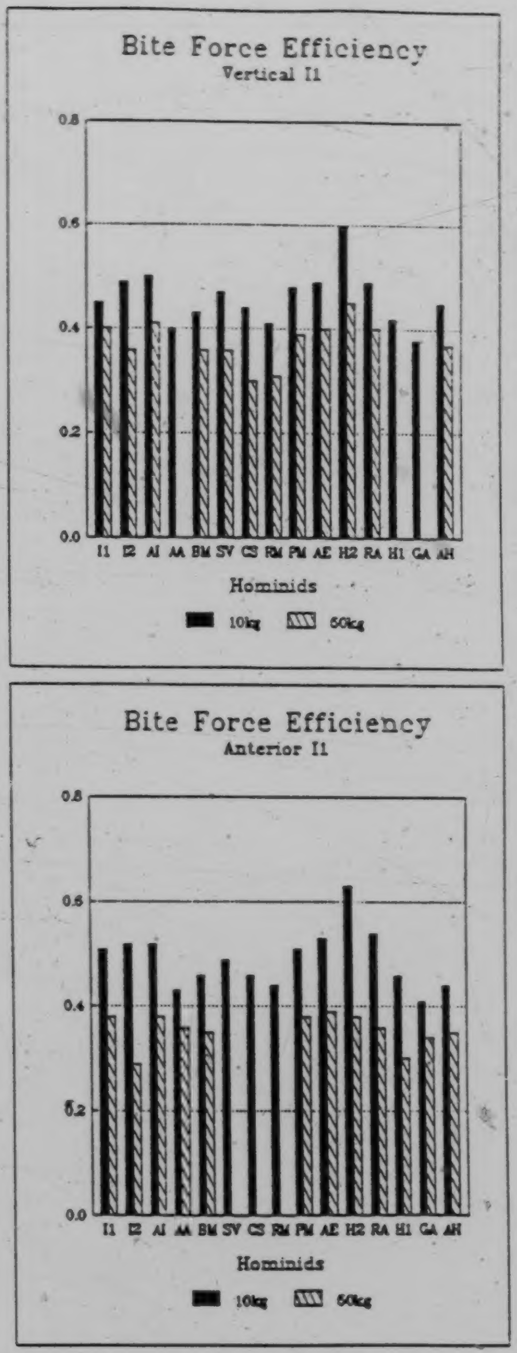


Fig. 69 Bite force efficiency of the hominids for selected incisor bites (missing bars indicate no solution to the problem).

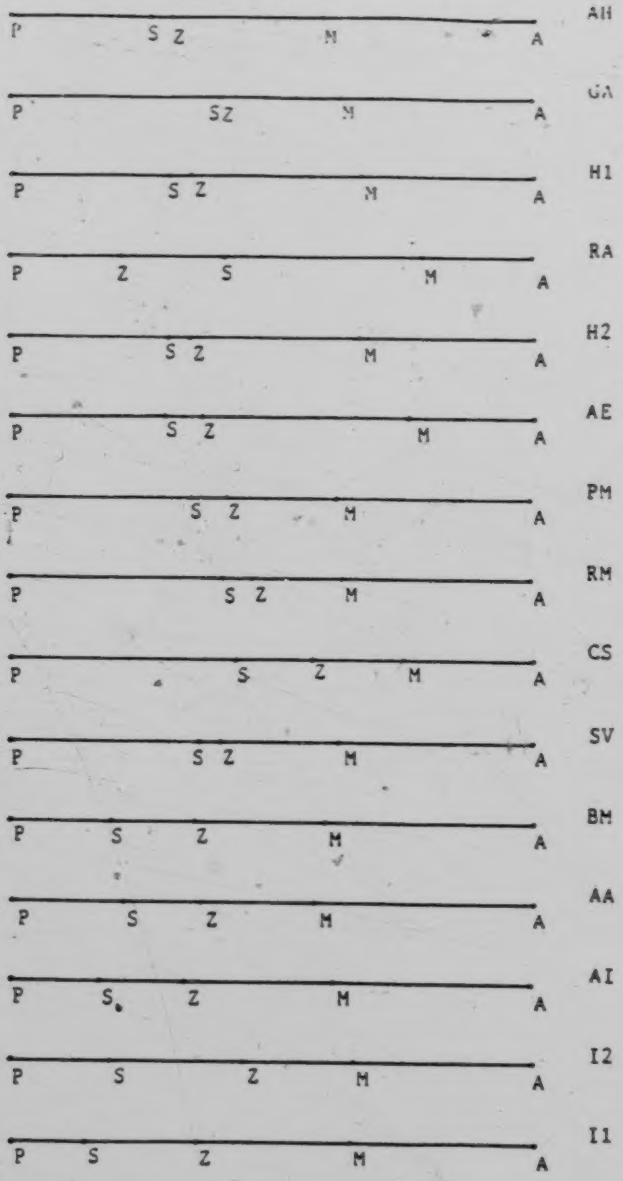

P S Z M A AH
P SZ M A GA
P S Z M A H1
P Z S M A RA
P S Z M A H2
P S Z M A AE
P S Z M A PM
P S Z M A RM
P S Z M A CS
P S Z M A SV
P S Z M A BM
P S Z M A AA
P S Z M A AI
P S Z M A I2
P S Z M A I1

Fig. 70 The proportions of the masticatory systems of the hominids in the sagittal plane. A, the position of the articular tubercle; M, the position of the third molar; P, the position of the most anterior point on the alveolus between the central incisors (prosthion); S, the most posterior point on the face (sellion); Z, the position of the zygomatic tubercle.

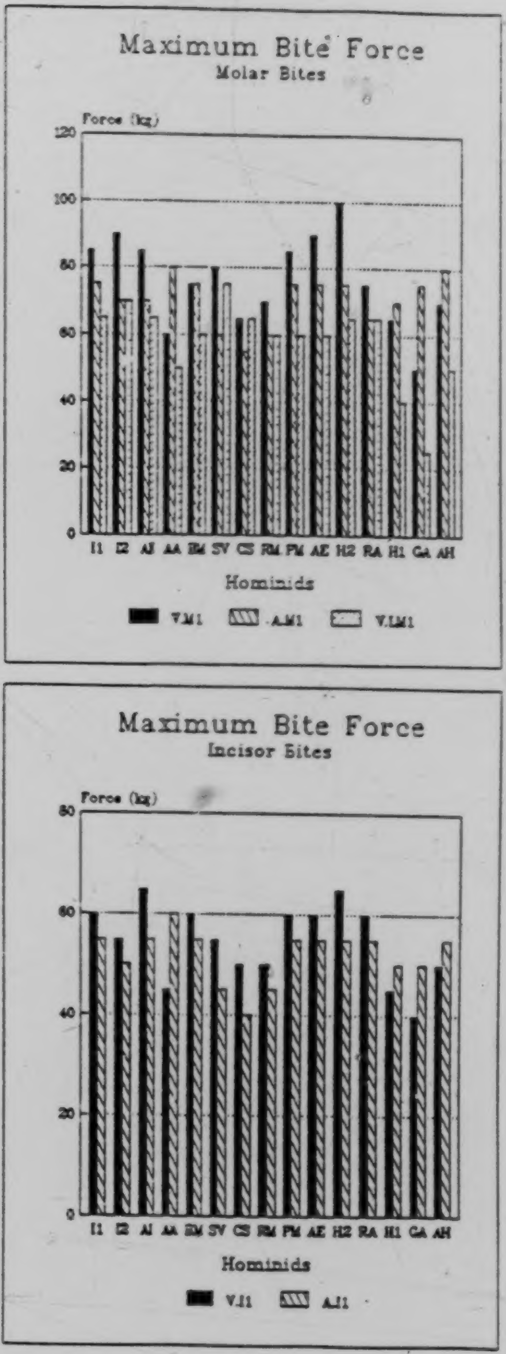


Fig. 71 Maximum bite force of the hominids for the vertical (V) and anterior (A) bites.

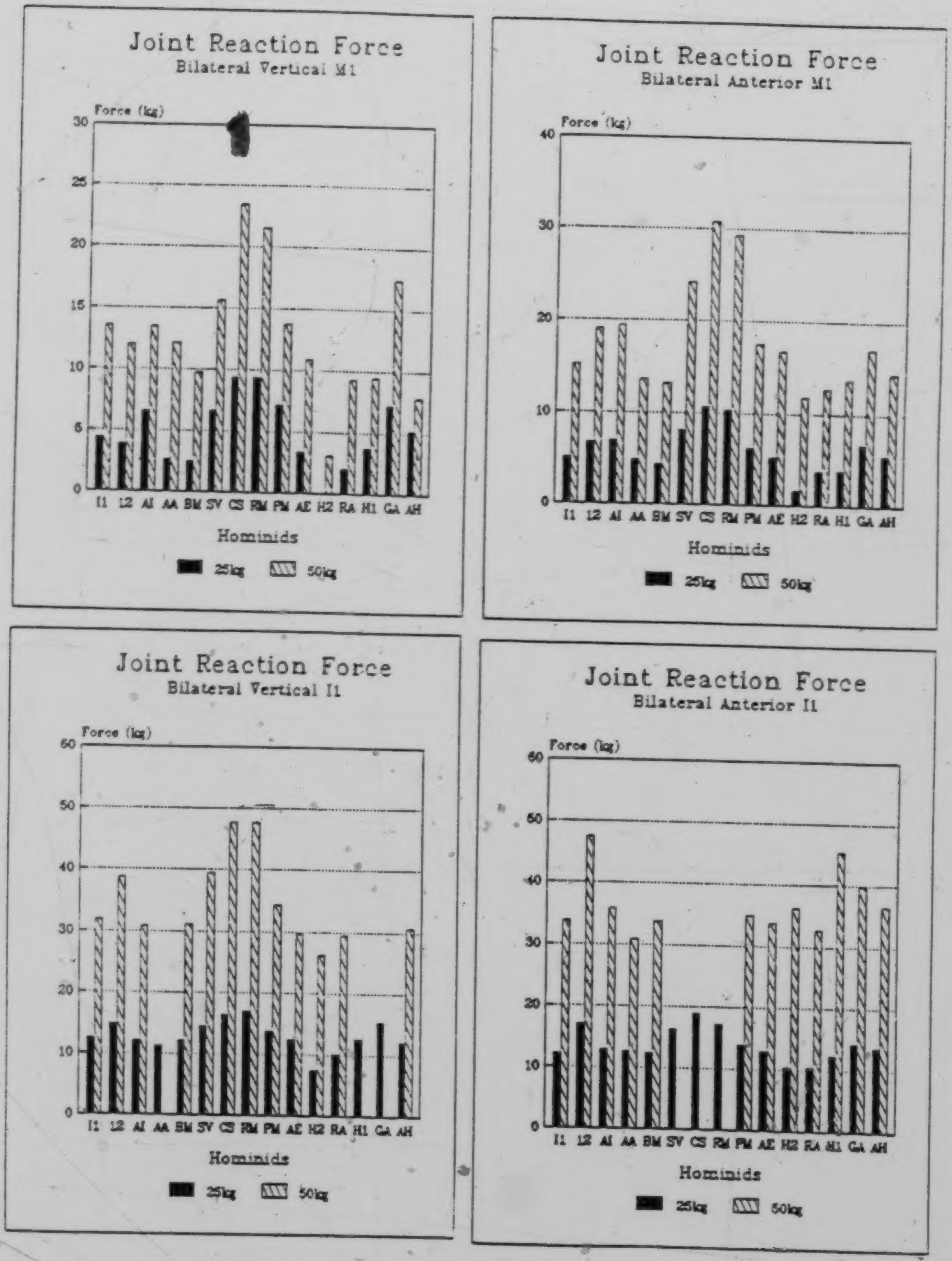


Fig. 72 Joint reaction forces of the hominids for selected bilateral bite forces.

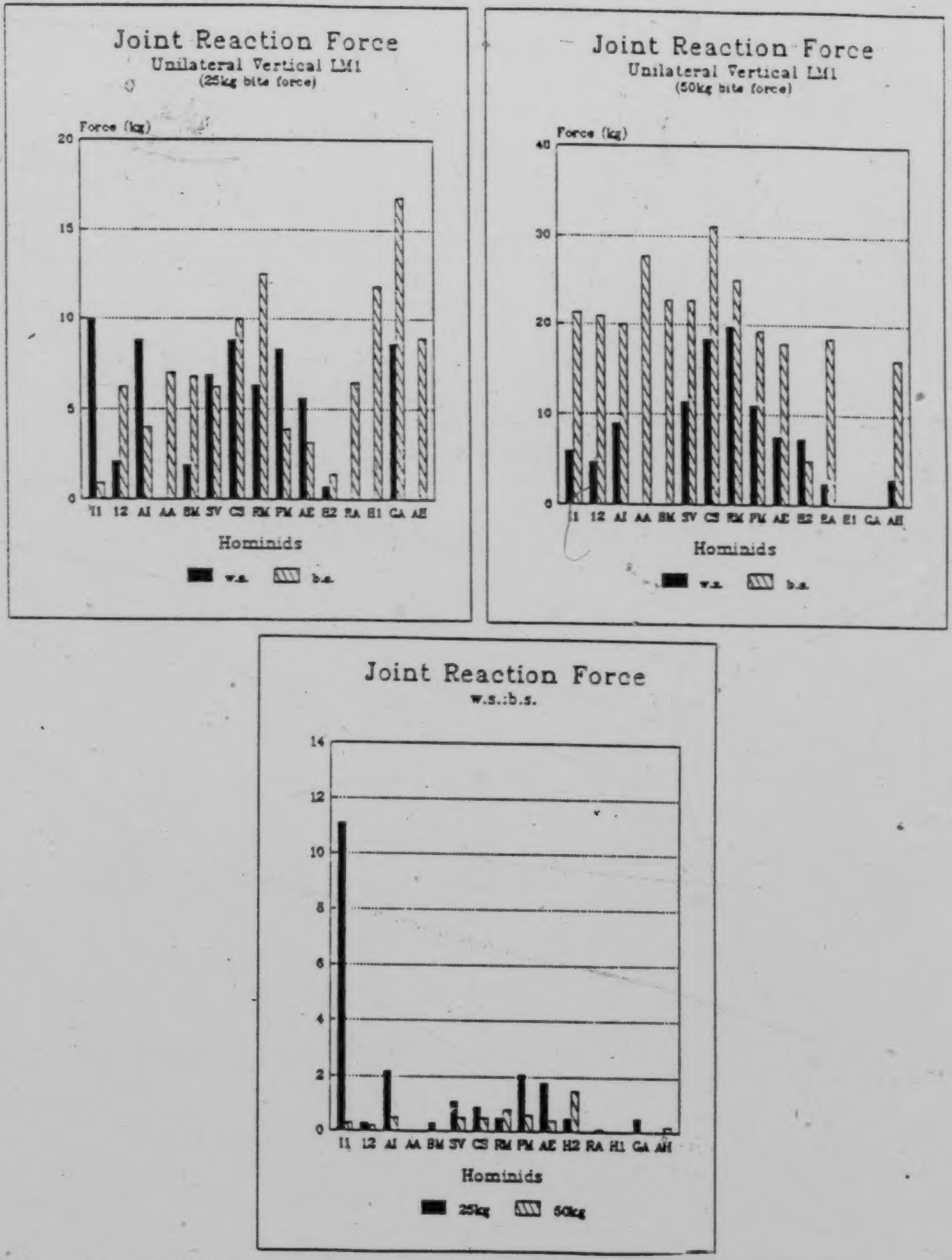


Fig. 73 Joint reaction forces of the hominids on the working side (w.s.) and balancing side (b.s.) for selected unilateral bite forces (above). Below, the ratio of the w.s. to b.s. joint reaction forces for those same bite forces.

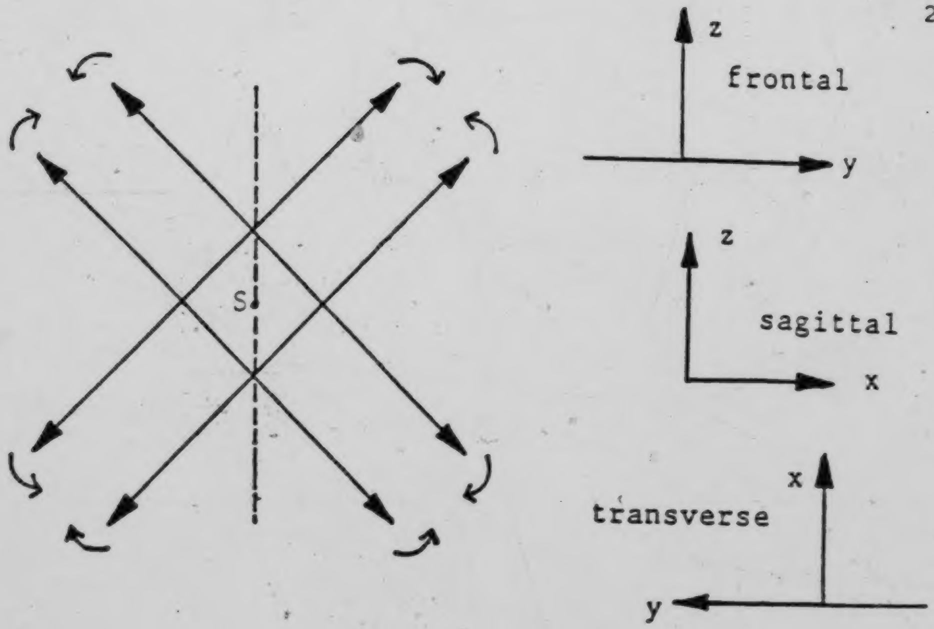


Fig. 74 The rotation about an axis caused by muscles having different directions and points of application. For the x component the torque is viewed in the frontal (yz) plane. The points of application of the right muscles are always to the right of the symphyseal point, S, (to the left of the dashed line). If the line of action of the muscle passes above the symphyseal point then the x component of torque is negative (directed into the page) if the muscle is directed inward, and positive (directed out of the page) if the muscle is directed outward.

For the y component, the torque is viewed in the sagittal (xz) plane. The points of application of the muscles are always behind the symphyseal point (to the left of the dashed line). If the line of action of the muscle passes above the symphyseal point then the y component of torque is negative (directed out of the page) if the muscle is directed forward, and positive (directed into the page) if it is directed backward.

For the z component the torque is viewed in the transverse (xy) plane. The points of application of the right muscles are always to the right and behind the symphyseal point (to the right of the dashed line). If the line of action of the muscle passes anterior to the symphyseal point then the z component of torque is positive (directed out of the page) if it is directed inward, and negative (directed into the page) if it is directed outward.

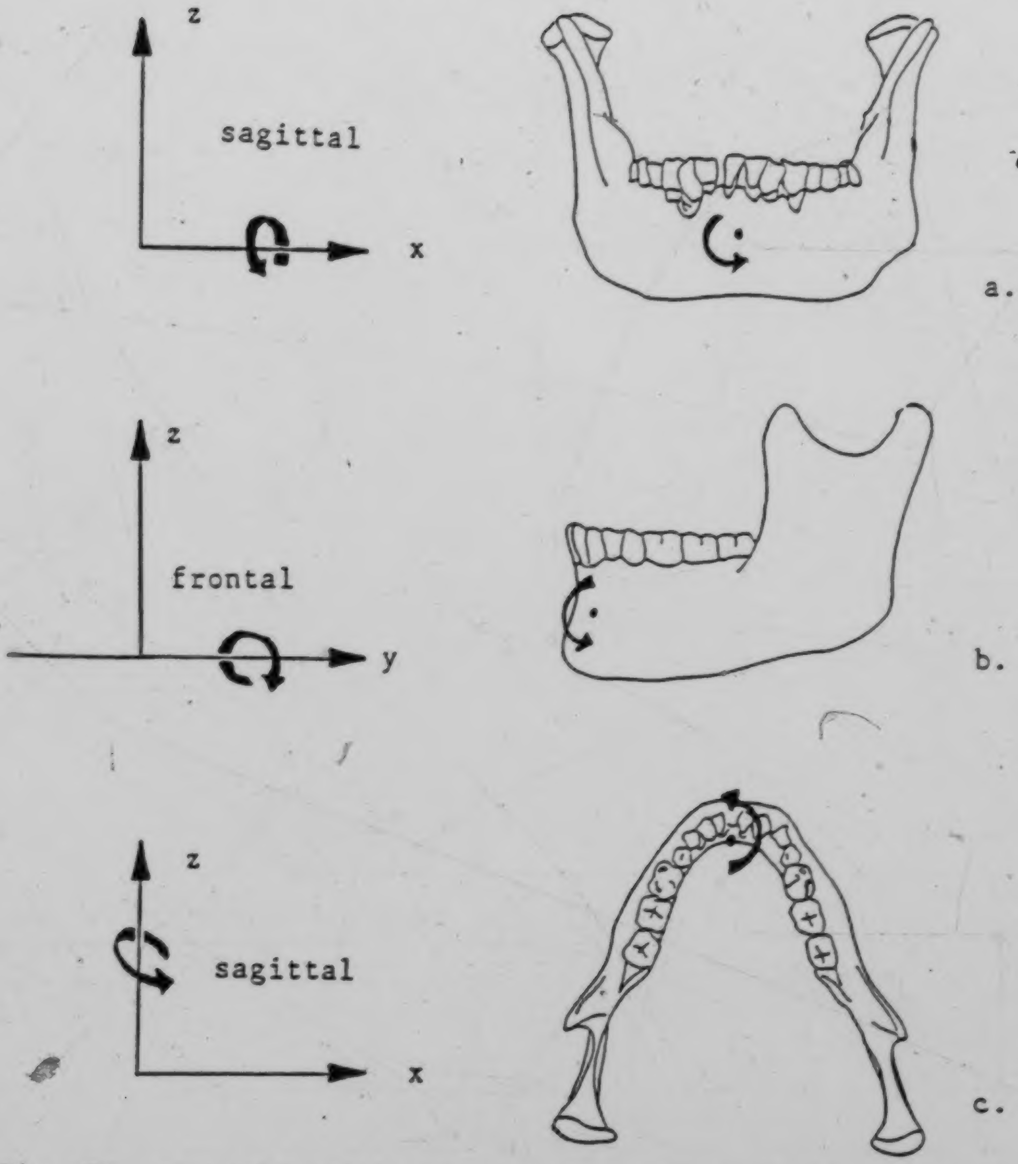


Fig. 75 a. When the x component of torque is positive it is directed forward and it causes the symphysis to be twisted about the horizontal axis such that on the right side the upper border is tensed and the lower border is compressed. b. When the y component of torque is positive it is directed medially on the right side and causes the symphysis to be twisted about a transverse axis such that the upper border is everted and the lower border inverted. c. When the z component of torque is positive it is directed upward and causes the symphysis to be twisted about a vertical axis such that on the right side the labial surface is compressed and the lingual surface is tensed.

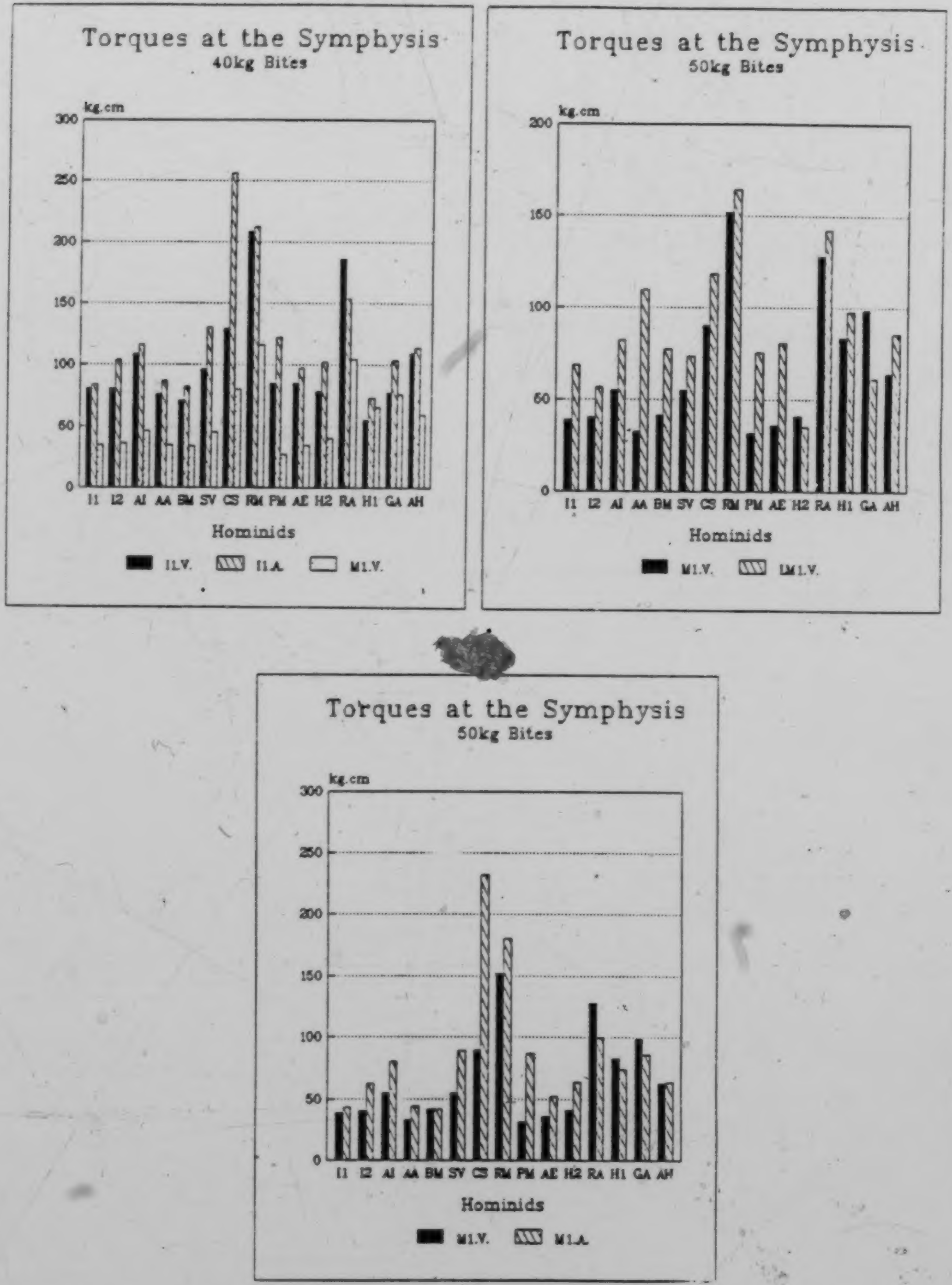


Fig. 76 Total torque at the symphysis for selected incisor and molar bites. V., vertical; A., anterior.

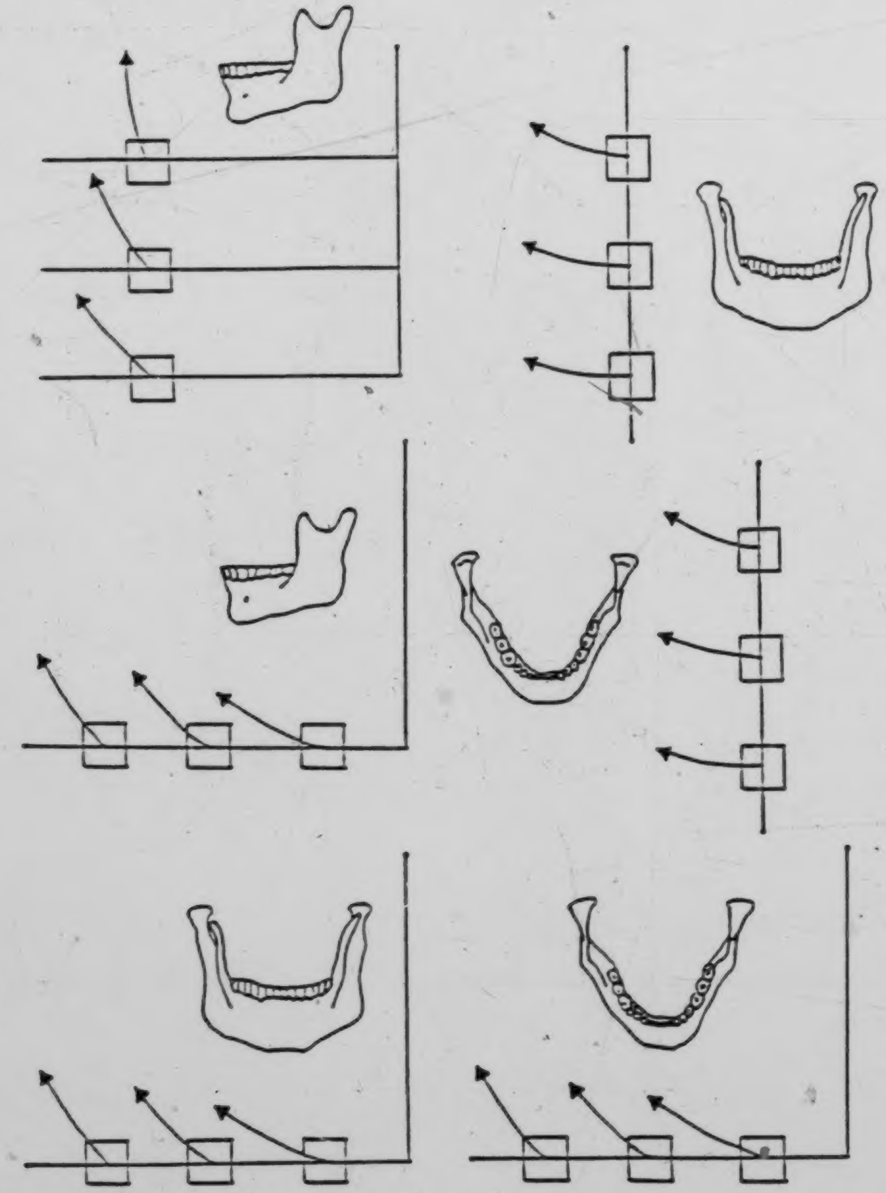


Fig. 77 Effect of the position of the condyle on the vertical, horizontal and transverse components of the path of closure of a mandibular tooth. Above, the effect of h in the sagittal (left) and frontal (right) planes; middle, the effect of r in the sagittal (left) and transverse (right) planes; below, the effect of b in the frontal (left) and transverse (right) planes.

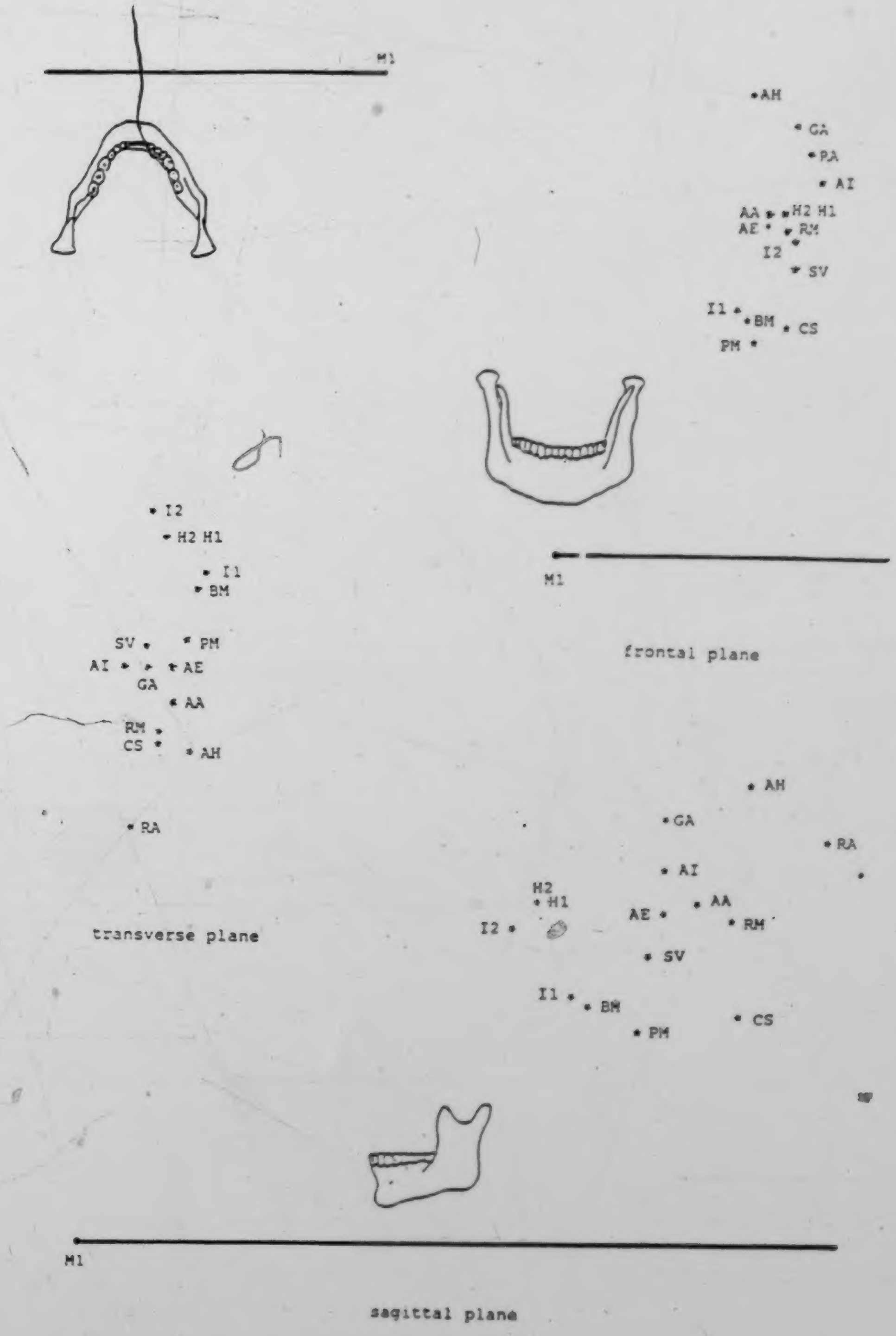

M1
AH
GA
RA
AI
AA
H2 H1
AE
RM
I2
SV
I1
BM
CS
PM
M1
frontal plane
I2
H2 H1
I1
BM
SV
PM
AI
AE
GA
AA
RM
CS
AH
RA
transverse plane
AH
GA
RA
AI
H2
H1
AA
AE
I2
RM
SV
I1
BM
CS
PM
M1
sagittal plane

Fig. 78 The position of the joint in three dimensions.

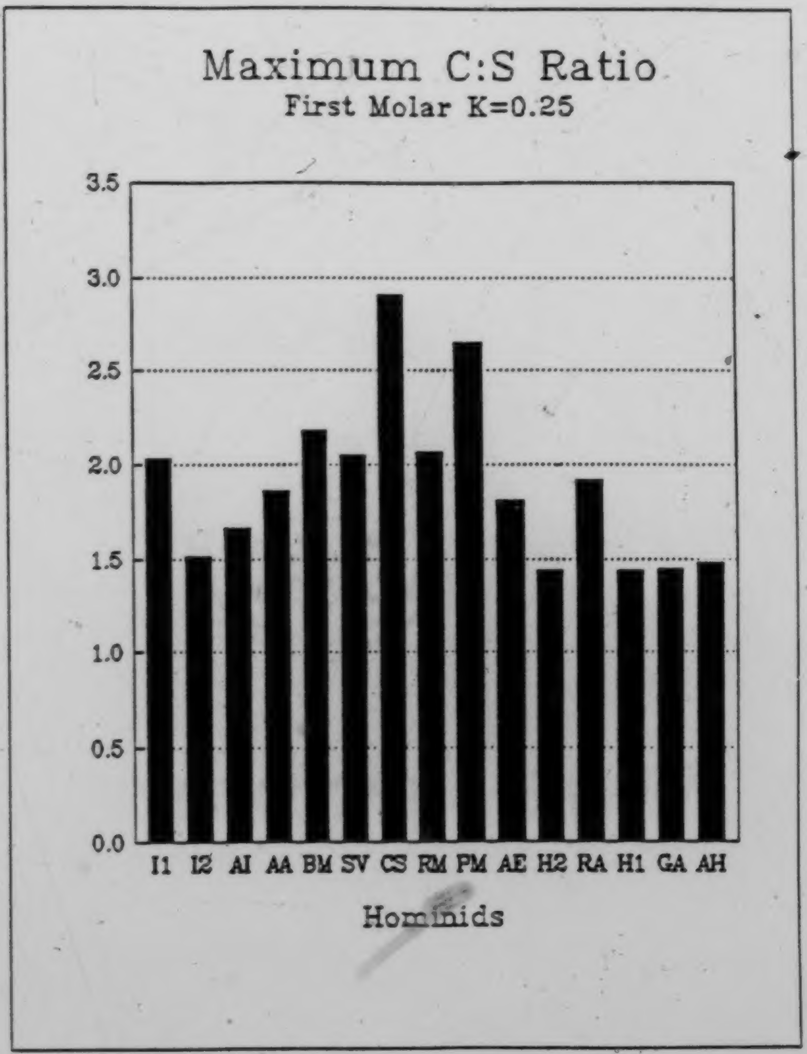


Fig. 79 Maximum crush:shear ratio for the first molar. K=0.25.

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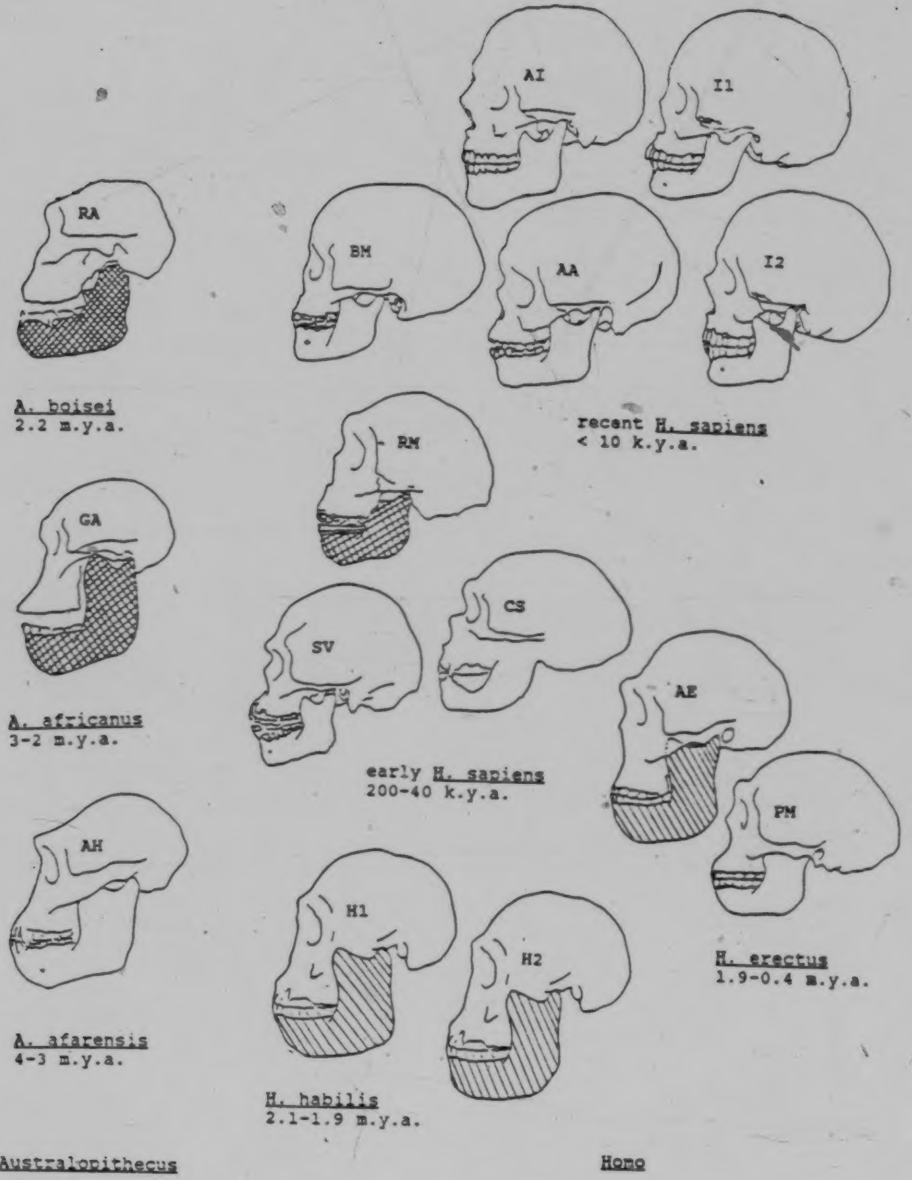
RA
A. boisei
2.2 m.y.a.
GA
A. africanus
3-2 m.y.a.
AH
A. afarensis
4-3 m.y.a.
AI
I1
BM
AA
I2
recent H. sapiens
< 10 k.y.a.
RM
SV
CS
early H. sapiens
200-40 k.y.a.
AE
PM
H. erectus
1.9-0.4 m.y.a.
H1
H2
H. habilis
2.1-1.9 m.y.a.
Australopithecus
Homo